CRYPTOGAMIC BOTANY

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CRYPTOGAMIC BOTANY

VOLUME I

BY

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Stanford University

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PREFACE

This book is designed for students who have had an introductory course in botany and who wish to make a more detailed study of plants below the level of seed plants. It is written from the standpoint that a thorough knowledge of a representative series in each of the major groups is better than scraps of information about a large number. This has been done with full knowledge of the danger of presenting the subject through a series of "types" and with a full realization that students are apt to substitute the type for the group and to consider all Equisetinae identical with *Equisetum*, all Marchantiales identical with *Marchantia*, and all Ulotrichaceae identical with *Ulothrix*. However, it is hoped that the introductory discussion to classes, orders, and families will help call attention to those characters of the selected representatives which are of distinctive importance and those which are special to the representative itself. In certain cases, as with the diatoms and the slime molds, it has been thought more advantageous to present the group as a whole instead of discussing selected representatives.

An attempt has been made to make the space devoted to each group proportional to its complexity and diversity, and to check the natural tendency to overemphasize groups in which an author is especially interested. I realize that some botanists will disagree with the allocation of space, especially in the relative proportions devoted to the algae and to the fungi. There has also been the problem of selecting the representatives for each of the groups. Wherever possible the genera selected are found in the United States and are of widespread distribution. In some cases this has meant the selection of a highly specialized rather than a generalized type of representative, but it is felt that the availability of material for study in the laboratory offsets this disadvantage.

Any general discussion of a group involves inclusion of subjects that are a matter of controversy. An attempt has been made to present both sides of controversial subjects, but I have not hesitated to express an opinion upon the relative merits of the arguments. Organization of a natural system of classification necessitates a consideration of phylogeny, a subject upon which no two botanists are in entire accord. Phyletic diagrams are included in this book because it is thought that a graphic presentation is the best method by which the student may visualize the suggested interrelationships. However, they are presented with a full realization that every botanist will disagree in minor or in major points.

The bibliography included in the book is looked upon as indicating the sources where a student may find a fuller discussion of the various subjects rather than as a documentation justifying the various statements. Adequate reference to the entire literature would have involved an expansion inappropriate to a book of this kind. Wherever possible, the references selected are to journals with a wide circulation in this country.

A large proportion of the figures have been especially drawn for this book. Figures designated as *semidiagrammatic* are those in which it has been impossible to draw all details of a preparation cell for cell. Figures designated as *diagrammatic* are more or less conventionalized drawings based upon one or more preparations. Theoretical drawings not based upon any particular preparation or preparations are designated as *diagrams*. Illustrations taken from other authors are designated as *from* when copied in facsimile, and as *after* when redrawn for this book. A large majority of the original drawings have been made by the author. Most of the habit sketches of red and brown algae were drawn by Mrs. Carl F. Janish and Mrs. Fred Addicott; the habit sketches of fungi were drawn by Mrs. Janish.

The completeness of the series of original illustrations is due to the courtesy of other botanists in furnishing material and preparations. Professors E. M. Gilbert and J. I. W. McMurphy have furnished preparations of many fungi; and Dr. D. A. Johansen has allowed me to select many special preparations of algae and fungi from his extensive collection. Professor D. H. Campbell has supplied preparations of *Chara;* Professor A. W. Haupt, preparations of *Zonaria;* Professor G. J. Hollenberg, preparations of *Polysiphonia;* Dr. H. C. Gilbert, preparations of *Ceratiomyxa;* Professor G. W. Keitt, preparations of *Venturia;* Professor J. G. Dickson, preparations of *Puccinia* and *Ustilago;* and Dr. B. O. Dodge, preparations of *Kunkelia.*

Many of the figures are based upon preparations made especially by Dr. Johansen, whose technical skill in sectioning and staining refractory tissues has made possible illustrative material that would otherwise have been unavailable.

I am also under deep obligation to Professor W. R. Taylor for a critical reading of the chapter on the red algae; and to Miss Ruth Daniels for her assistance and painstaking care in preparing for publication the final draft of the manuscript.

March, 1938.

CONTENTS

PAGE

PREFACE v

CHAPTER I

THE CLASSIFICATION OF SPORE-PRODUCING PLANTS 1

CHAPTER II

CHLOROPHYTA 12

CHAPTER III

EUGLENOPHYTA 113

CHAPTER IV

PYRROPHYTA 151

CHAPTER V

CHRYSOPHYTA 168

CHAPTER VI

PHAEOPHYTA 220

CHAPTER VII

CYANOPHYTA 277

CHAPTER VIII

RHODOPHYTA 295

CHAPTER IX

MYXOTHALLOPHYTA 351

CHAPTER X

EUMYCETAE—INTRODUCTION 366

CHAPTER XI

PHYCOMYCETAE 371

PAGE

CHAPTER XII

ASCOMYCETAE 415

CHAPTER XIII

BASIDIOMYCETAE. 466

CHAPTER XIV

FUNGI IMPERFECTI. 511

CHAPTER XV

LICHENS 513

INDEX 525

CRYPTOGAMIC BOTANY

VOL. I

CHAPTER I

THE CLASSIFICATION OF SPORE-PRODUCING PLANTS

The classification of plants has undergone many changes since Aristotle (384–322 B.C.) and his pupil Theophrastus (372–287 B.C.) first grouped them into *trees*, *shrubs*, and *herbs*. Beginning with the herbalists of the sixteenth century, there came a gradual realization that the most obvious characters are not necessarily the most important. Their gradual recognition that the structure of the flower is of more fundamental importance in classification than are vegetative characters paved the way for the "sexual system" of Linnaeus in which he grouped plants according to the number of stamens and carpels, their union, and their presence or absence in the flower. This system, although wholly artificial, had the great advantage that an unknown plant, when discovered, could be easily interpolated among those already known. Linnaeus divided the plant kingdom into 25 classes, one of which, the *Cryptogamia*, included all plants with "concealed" reproductive organs. He[1] characterizes the class as follows: "*CRYPTOGAMIA continet Vegetabilia, quorum Fructificationes oculis nostris se subtrahunt, & structura ab aliis diversa gaudent.*" He divided the Cryptogamia into the following four orders: *Filices* which included all known pteridophytes; *Musci* which included all known mosses and leafy liverworts; *Algae* which included algae, lichens, and thallose liverworts; and the *Fungi*.

Natural systems of classification, that is, those in which plants were grouped according to what were thought to be their natural affinities, were established long before Darwin proposed the evolutionary theory. The first natural system, that of de Jussieu,[2] divided plants into three major groups, *Acotyledones*, *Monocotyledones*, and *Dicotyledones*. His Acotyledones are the approximate equivalent of Linnaeus' Cryptogamia, and the various orders he recognized among the Acotyledones are equally

[1] Linnaeus, 1754. [2] De Jussieu, A. L., 1789.

heterogeneous. Many other natural systems for the classification of plants were proposed during the first half of the nineteenth century, but all of them[1] are very inadequate as far as the spore-producing (cryptogamic) plants are concerned. The inadequate treatment of cryptogamic plants was due in large part to an almost complete lack of knowledge concerning their development and life cycles. In 1851 this condition changed overnight with the publication of Hofmeister's epoch-making studies on the life histories of a wide variety of bryophytes and pteridophytes.[2] He was the first to show that the life cycle in bryophytes, pteridophytes, and conifers involves an alternation of generations and that there are certain fundamental similarities and differences in general structure of reproductive organs produced during the life cycle in each of the three. About the same time phycologists and mycologists were beginning studies on the reproduction and the life histories of algae and fungi that brought out their distinctive features.

The decade following Darwin's announcement of the theory of evolution in 1859 is marked by the appearance of true natural systems in which the fundamental basis for the classification of plants is phylogeny and in which they are ranged in an ascending series from the most primitive to the most advanced. The system proposed by Eichler[3] in 1886 was widely adopted and is still followed in more or less modified form in many present-day textbooks. As originally proposed by Eichler, this system divided the plant kingdom as follows:

A. CRYPTOGAMAE

Division I. Thallophyta
 Class 1. Algae
 Class 2. Fungi
Division II. Bryophyta
Division III. Pteridophyta

B. PHANEROGAMAE

Division I Gymnospermae
Division II. Angiospermae
 Class 1 Monocotyleae
 Class 2. Dicotyleae

Validity of the Thallophyta. Plants placed in the Thallophyta may be distinguished from other plants on the basis of structure of their gamete- and spore-containing organs. Sex organs of Thallophyta are one-celled, or, when multicellular (as in certain brown algae), they do not have the gametes surrounded by a layer of sterile cells. Bryophytes and pteridophytes have multicellular sex organs in which there is an outer

[1] See Lindley, 1847, for a summary of the various systems.
[2] Hofmeister, 1851, 1862. [3] Eichler, 1886.

layer of sterile cells. Sporangia of Thallophyta are always one-celled; those of higher plants are always many-celled. Another distinction between Thallophyta and other plants is the fact that zygotes of Thallophyta never develop into multicellular embryos while still within the female sex organs.

Granting the distinctiveness of the assemblage of plants called the Thallophyta there then arises the question: Is this a natural division of the plant kingdom and one that may, in turn, be divided into *Algæ* and *Fungi*? To accept the Thallophyta as a natural division of the plant kingdom implies acceptance of the view that both the algae and the fungi are each a more or less homogeneous phylogenetic series. The question of phylogenetic interrelationships between the algae rests, in turn, upon determination of an adequate basis for classifying them. The test of time has shown the inadequacy of classification of thallophytes based either upon the vegetative structure or the methods of reproduction.

It has become increasingly clear during the past quarter century that the morphology and the physiology of the individual cells are the fundamental bases upon which the algae must be classified. This evidence shows that there are several series among the algae, each of which has cells with certain distinctive physiological and morphological traits. Chief among the morphological characteristics is the structure of the motile cell, and for most of the series among the algae there is a striking constancy in its organization, especially with respect to the number, arrangement, and relative length of the flagella. On the physiological side there is, throughout each series, a constancy in the pigments present in the plastids and a constancy in the chemical nature of the food reserves accumulating through photosynthetic activity. For example, the green algae (Chlorophyta) almost always have flagella of equal length, a predominance of green pigments in their plastids, and usually store photosynthetic reserves as starch. On the other hand, the yellow-green algae (Xanthophyceae) always have flagella of unequal length, have a predominance of carotinoids in their plastids, do not form starch, and usually store photosynthetic reserves as oils. This constancy with which the morphological and physiological characteristics obtain in each series and the marked differences between the various series (Chlorophyta, Cyanophyta, Phaeophyta, etc.) suggest very strongly that the various major groups of algae have but little in common with one another.

Acceptance of the view that the various series of algae are more or less independent of one another means that both the Thallophyta and its subdivision Algae must be abandoned as natural units in classifying plants. This necessitates giving all or certain of the classes among the Algae a correspondingly greater rank. Abandonment of the Algae as a subdivision of the plant kingdom does not mean that the word *alga* must

be abandoned. It is still of great service as a descriptive term for designating simple plants with an autotrophic mode of nutrition.

The taxonomic disposition of the Fungi, the other subdivision of the Thallophyta, depends upon the question of their origin. This is highly controversial and opinion is divided as to whether they arose from the protozoa or whether they had either a monophyletic or polyphyletic origin among the algae. If they arose from protozoa, they should be put in one or more divisions coordinate in rank with the various algal divisions; if they arose from the algae, they should be placed as classes of one or more of the algal divisions.

Flagellates and Algae. Although it is quite easy to think of the algae or protophyta as a heterogeneous assemblage of simple plants, it is much more difficult to state precisely just what organisms belong to this assemblage. The older distinctions between the plant and animal kingdoms (based upon motility, nutrition, and the presence of a cell wall) break down completely when applied to unicellular organisms, and it is quite impossible to establish criteria that will differentiate in a clear-cut manner between protophyta and protozoa.

The first breakdown of the distinction between *Flagellata* and *Algae* was the demonstration that the Volvocales belong to the green algae (Chlorophyta) and are the starting point for the evolution of them Later there was a discovery that the chrysomonads, the dinoflagellates, and certain other pigmented flagellates were each related to organisms of a truly algal type. This demonstration of a phylogenetic connection between most of the unicellular pigmented flagellates and evident algae might be used as an argument for placing all pigmented protista among the algae or protophyta. At first glance such an argument appears to be quite logical, but it immediately leads to other difficulties, since it involves an inclusion of phylogenetic series in which evolution has been more toward an animal-like than a plant-like organization. It is, therefore, more convenient to take a somewhat arbitrary stand and to include among the algae only those pigmented flagellates in which there has been an evident evolution of plant-like forms.

Validity of the Pteridophyta. For a long time the pteridophytes were thought to be sharply delimited from gymnosperms and angiosperms because of their lack of seeds. Paleobotanical research during the past 40 years has tended to break down this distinction by bringing to light a number of extinct plants that were distinctly pteridophytic in vegetative organization but were seed bearing.

For a long time, also, the pteridophytes were thought to be a more or less homogeneous series, as is evidenced by the calling of them the "ferns and fern allies." Comparative morphological studies and study of the vascular organization of the mature sporophyte have shown that the

lycopods, the horsetails, and the true ferns constitute three independent series. Paleobotanical research has shown that the three evolved simultaneously from an ancient extinct group of pteridophytes known as the *psilophytes*. Neither the lycopod series nor the horsetail series evolved to a point where there were true seed-bearing plants. The true fern series lies along the evolutionary line leading to the seed plants. The geological record of the seed plants is as ancient as that of the true ferns, and it has been thought[1] that seed plants originated along the line leading to the true ferns rather than directly among them.

Because of this heterogeneity among the pteridophytes and because spermatophytes seem to have been evolved only along the filicinean line, there has been a recent tendency to abandon the Pteridophyta and the Spermatophyta as divisions of the plant kingdom. All of those proposing such a change divide the vascular plants into four groups: the Psilophyta (Psilopsida) which include the psilophytes; the Lycopsida which include the lycopodian series; the Sphenopsida which include the horsetails; and the Pteropsida which include the ferns, gymnosperms, and angiosperms. There is not an equal unanimity of opinion concerning the rank the four groups should be accorded. According to one proposal[2] they should be considered four divisions replacing the old Pteridophyta and Spermatophyta; according to another[3] they should be considered classes of a single division (Tracheophyta) replacing the Pteridophyta and Spermatophyta.

The placing of ferns and seed plants in a single series called the Pteropsida has the advantage of showing that the phylogenetic connections of seed plants are with the ferns rather than with other pteridophytes. However, it obscures the fact that gymnosperms and angiosperms are distinct from ferns and that they are not immediately derived from them. It also obscures the fact that evolution of the ferns attained about the same level as that found in the lycopodian and the equistaceous series. In view of the foregoing the retention of the Pteridophyta as a natural division of the plant kingdom seems justified. Retention of the Pteridophyta as a distinct division is decidedly advantageous in accentuating the fact that the three prominent series among them (lycopods, horsetails, and true ferns) are evolutionary side lines that do not lead to the predominant element in present-day land vegetation—the seed plants.

Classification of Spore-producing Plants. According to the International Rules of Botanical Nomenclature, the primary step in a classification of the plant kingdom is the establishment of divisions. The foregoing discussion has attempted to show that the Thallophyta should not be recognized as a division of the plant kingdom and that the Pteridophyta should be recognized. There then arises the question, How

[1] Scott, 1923. [2] Zimmermann, 1930. [3] Eames, 1936.

many divisions are necessary for an adequate classification of plants below the level of seed plants?

The subdivision Algae of the division Thallophyta has long been divided into a number of classes. Recent discussions of the phylogeny and classification of algae[1] hold that certain of the classes are sufficiently distinct from one another to warrant recognition as divisions of the plant kingdom. However, certain other classes have so many features in common that they are evidently related to one another. For example the yellow-green algae (Xanthophyceae or Heterokontae), the golden-brown algae (Chrysophyceae), and the diatoms (Bacillariophyceae) have so many common features that they may be placed in a single division, the Chrysophyta.[2] These common features include: cell walls composed of two overlapping halves, silicified cell walls, motile cells with similarities in flagellation, similarities in pigmentation of chromatophores, similarities in nature of food reserves, and a distinctive endoplasmic type of resting spore (cyst). The affinities between the Cryptophyceae (cryptomonads) and the Dinophyceae (dinoflagellates) also seem strong enough to warrant placing them in a single division, the Pyrrophyta.[3] On the other hand, the grass-green algae (Chlorophyceae), the euglenoids (Euglenophyceae), the brown algae (Phaeophyceae), the blue-green algae (Myxophyceae), and the red algae (Rhodophyceae) each seem so distinctive that they should be placed in a separate division. Thus, the number of divisions necessary for an adequate classification of the algal portion of the plant kingdom is less than the number of classes among the old subdivision Algae.

For reasons which will be given later (page 368), it seems more probable that the fungi evolved from protozoa rather than from algae. They should, therefore, be included in a division or divisions distinct from any of those to which algae are referred.

The foregoing suggested substitution of a number of divisions for the Thallophyta, together with a retention of the Bryophyta and Pteridophyta, seems to afford a natural classification of plants other than seed plants. These divisions are:

Chlorophyta, or grass-green algae, in which the protoplasts have definite plastids that contain the same photosynthetic pigments as do vascular plants and in the same proportions. Most Chlorophyta accumulate starch as the photosynthetic reserve. Motile reproductive cells are usually bi- or quadriflagellate. The flagella are borne at the anterior end of a cell and, with a few minor exceptions, are equal in length. Reproduction may be sexual or asexual. The gametes are always produced within unicellular sex organs, and a fusing pair may be of equal or unequal size. The division includes approximately 5,700 species.

[1] Fritsch, 1935; Pascher, 1931; Smith, G. M., 1933. [2] Pascher, 1914, 1921.
[3] Pascher, 1914, 1927.

Euglenophyta, or euglenoids, in which the only pigments are chlorophyll and carotinoids. The pigments, if present, are localized in grass-green chloroplasts. The reserve foods include both paramylum (an insoluble carbohydrate related to starch) and fats. Almost all members of the division are naked unicellular flagellates. Motile cells have one, two, or three flagella. Reproduction is generally by cell division but may be by means of thick-walled resting stages (cysts). Sexual reproduction is definitely established for one genus only. The division includes approximately 335 species.

Pyrrophyta which include the cryptomonads and the dinoflagellates. Their cells have photosynthetic pigments localized in yellowish-green to golden-brown chromatophores. Photosynthetic reserves generally accumulate as starch or starch-like compounds, but they may also accumulate as oil. Cell walls, when present, generally contain cellulose. Most members of the division are unicellular biflagellated organisms in which the two flagella are usually dissimilar in form, position, and motion. Some genera are without flagella, alga-like, and either unicellular or multicellular. Immobile genera may reproduce asexually by means of either motile or nonmotile spores. Sexual reproduction is found in but two or three genera. The division includes approximately 1,000 species.

Chrysophyta which include the yellow-green algae (Xanthophyceae), the golden-brown algae (Chrysophyceae), and the diatoms. Their cells have the photosynthetic pigments localized in definite chromatophores in which there is a preponderance of yellowish or brownish carotinoid pigments. The food reserves include both oils and leucosin (an insoluble carbohydrate of unknown composition). There is never a formation of starch. The cell wall is usually composed of two overlapping halves, and it is frequently impregnated with silica. The cells may be flagellated or nonflagellated and solitary or united in colonies of definite form. Asexual reproduction of immobile genera may be by means of flagellated or nonflagellated spores. There is a widespread, although not universal, endoplasmic formation of a unique type of spore—the statospore. Sexual reproduction, when present, is by a fusion of flagellated or nonflagellated gametes of equal size. The division includes approximately 5,700 species.

Phaeophyta, or brown algae, which have their photosynthetic pigments localized in chromatophores that also contain a golden-brown pigment, *fucoxanthin*. The chief food reserve is a soluble dextrin-like polysaccharide, laminarin. The plant body is always immobile, multicellular, and generally of a definite macroscopic form. Motile reproductive cells, whether sexual or asexual, are pyriform and have two laterally inserted flagella of unequal length. The life cycle generally involves an alternation of a diploid asexual generation with a haploid sexual generation. Both generations are free-living, and the two may be similar or dissimilar. The division includes approximately 900 species.

Cyanophyta, or blue-green algae, in which the photosynthetic pigments are distributed throughout the entire peripheral portion of a protoplast and are not localized in definite plastids. In addition to chlorophyll and the accompanying carotinoids, a protoplast may contain a blue pigment (*phycocyanin*) and a red pigment. The Cyanophyta differ from all other algae in their primitive type of nucleus (the central body), which lacks a nuclear membrane and nucleoli. None of the Cyanophyta forms flagellated reproductive cells, and none of them reproduces sexually. The division includes approximately 1,400 species.

Rhodophyta or red algae in which the photosynthetic pigments are localized in chromatophores that contain a red pigment (*phycoerythrin*) and sometimes also a blue pigment (phycocyanin). The chief food reserve is an insoluble carbohydrate, floridean starch. The plant body is always multicellular and generally of a definite macroscopic form. Flagellated reproductive cells, either asexual or sexual, are not formed by red algae. Most genera reproduce sexually. Sexual reproduction is effected by passive transportation of nonflagellated male gametes to, and their lodgement against, the female sex organ, the carpogonium. The life cycle of many, although not all, Rhodophyta involves an alternation of a free-living haploid sexual generation with a free-living diploid sexual generation of identical form. The division includes approximately 2,500 species.

Myxothallophyta, or slime molds, in which there are no photosynthetic pigments and in which the plant body is a naked mass of protoplasm throughout all stages of vegetative development. The vegetative body may be either a single large multinucleate mass or an aggregation of many small uninucleate protoplasts. Reproduction is by the formation of many small uninucleate spores, each with a distinct wall. In a majority of the genera the spores are borne within or upon a fructification of definite form. The division includes approximately 435 species.

Eumycetae, or true fungi, in which there are no photosynthetic pigments and in which there is almost always a definite cell wall throughout all stages of vegetative development. All but the most primitive of the Eumycetae have the branching filamentous type of plant body known as a *mycelium*. It may consist of a single multinucleate cell or be transversely divided into many cells. The various branches (hyphae) of a mycelium may lie in an amorphous felt-like mass, or they may be intertwined to form a macroscopic mass of definite form. Reproduction is by means of a wide variety of types of spores, some of which are formed directly or indirectly after a union of gametes or gamete nuclei. The division, inclusive of lichens, contains approximately 89,000 species.

Bryophyta which include the liverworts, hornworts (anthocerotes), and mosses. The Bryophyta are simple green plants which differ from all

algae in that their sex organs are always multicellular and have an outer layer of sterile cells. The life cycle involves an alternation of a free-living haploid sexual generation (gametophyte) with a diploid asexual generation (sporophyte). The latter is completely or partially dependent upon the former throughout all stages of development. The internal organization of the sporophyte is always simple, and there is never a differentiation of vascular tissues. The division includes approximately 23,000 species.

Pteridophyta which includes the psilophytes, lycopods, horsetails, and true ferns. They are green plants distinguishable from Bryophyta by the

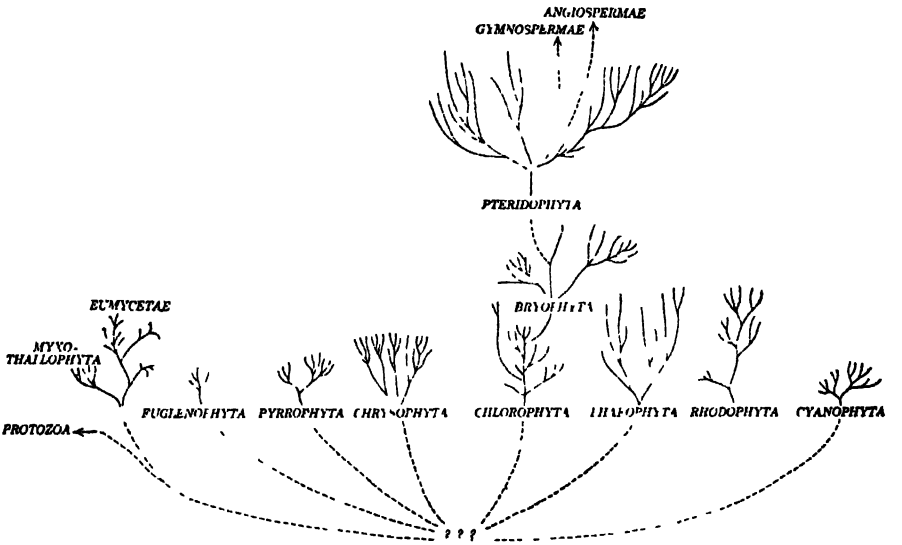


FIG. 1.—Diagram showing the suggested interrelationships of the divisions of the plant kingdom.

fact that the sporophyte is independent of the gametophyte at maturity. They differ from seed plants in their liberation of the spore, or the gametophyte developed from it, from the sporangium. Mature sporophytes have an internal vascular system composed of xylem and phloem. Generally, although not always, the sporophyte is differentiated into stem, leaf, and root. The division includes about 4,850 living species.

Interrelationships. The various algal divisions described on the preceding pages seem to be phyletic series entirely independent from one another. The answer to the question as to whether they arose independently or from some common ancestral stock is obscure and purely a matter of speculation. However, numerous physiological and morphological features common to the various algal series suggest that they may have had a common origin in some primitively organized ancestral stock. The common physiological features include ability to elaborate foods photosynthetically, ability to form enzymes, permeability, and similarities in

responses to external stimuli. Most of them also have such common morphological features as a differentiation of the protoplasm into cytoplasm and nucleus, a localization of the photosynthetic pigments in plastids, and a qualitative division of the nuclear material.

Evolution among the various series of algae has not reached the same stage of advancement. There has been but little vegetative advancement in either the Chrysophyta, the Pyrrophyta, or the Cyanophyta, and in all of them the reproductive organs are simple. The Phaeophyta and the Rhodophyta have attained a higher level in that certain of them have a relatively large plant body, complex in form and with some internal differentiation of tissues. However, in neither the red nor the brown algae does there seem to have been an evolution of a true land plant. Evolution of the Chlorophyta has progressed far beyond an algal organization of the plant body, and the reproductive structures typical for algae. This algal series seems to be the one giving rise to the bryophytes, pteridophytes, and all other true land plants.

The relationships of plants are usually shown by a diagram having the form of a many-branched tree. A more accurate diagrammatic representation of the evolutionary interrelationships among plants would be that of a tree surrounded by seven shrubs (Fig. 1). The tree would represent the Chlorophyta and the land plants derived from them. The shrubs would represent the other algae and the fungi. Three of the algal shrubs would be very low. The other two, representing the Phaeophyta and Rhodophyta, would be somewhat taller.

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CHAPTER II

CHLOROPHYTA

The Chlorophyta, or grass-green algae, have the same photosynthetic pigments (chlorophyll *a*, chlorophyll *b*, carotin, xanthophyll) as do the vascular plants and in the same propórtions. These pigments are localized in definite plastids (*chloroplasts*). Most of the Chlorophyta accumulate starch as the photosynthetic reserve. The plant body (*thallus*) may be unicellular or multicellular. Motile reproductive cells of Chlorophyta have their flagella, generally two or four, borne at the anterior end and, with a few exceptions, have all flagella equal in length. Reproduction may be asexual or sexual. When sexual reproduction takes place, the gametes are always produced within unicellular sex organs, and the fusing pair of gametes may be of equal or unequal size.

There are approximately 360 genera and 5,700 species of Chlorophyta. A large majority of the species are fresh-water in habit. Most of the fresh-water species are microscopic organisms; many of the marine species are large and macroscopically recognizable.

The Chlorophyta are divided into the two following classes:

Chlorophyceae, in which the plant body is unicellular or multicellular, but in which multicellular thalli never have growth initiated by an apical cell. The sex organs are unicellular, are borne freely exposed, and only in very rare cases become surrounded by a sheath of sterile cells after fertilization.

Charophyceae in which the plant body is always multicellular and in which growth is initiated by an apical cell. The sex organs are unicellular and are always borne within special sterile multicellular envelopes.

CLASS 1. CHLOROPHYCEAE

Thalli of Chlorophyceae may be unicellular, or they may be multicellular and have either a definite or an indefinite number of cells. Thalli with an indefinite number of cells may have them arranged in irregular masses, in filaments, in expanded sheets, or in solid or hollow cylinders. Many members of the class reproduce asexually by zoospores, aplanospores, or akinetes. Sexual reproduction is also of widespread occurrence and ranges from isogamy to oögamy. The sex organs are always one-celled and not surrounded by an envelope of sterile cells.

There are about 350 genera and 5,500 species of Chlorophyceae.

Occurrence and Distribution. Approximately 10 per cent of the species are marine, and most of them grow in the intertidal zone. Certain orders, as the Ulvales and Siphonales, are predominately marine; other orders have a few marine species; and still others, as Oedogoniales and Zygnematales, do not have marine species. A majority of the fresh-water species are submerged aquatics, but the number of species that do not grow submerged in water is surprisingly large. These include the species growing on soil, on rocks or cliffs, on damp woodwork or the bark of trees, and on snow or ice. There are also a few species that are internal parasites of land plants or epiphytes upon land animals.

Many of the marine species have a definite geographical distribution, which is primarily dependent upon temperature of the water. The same does not hold for fresh-water species, and, except for desmids and a few tropical species, all of them are cosmopolitan and may be expected anywhere.

Cell Structure. *The Wall.* With the exception of a few primitive genera, the protoplast lies within a definite wall. In the primitive genera without walls, the exterior of the naked protoplast is rigid and of a characteristic shape. The characteristic cell shape among genera with a wall is therefore probably due to the protoplast itself rather than to the enclosing wall. All cells surrounded by a wall have one composed of at least two concentric portions. The innermost portion is usually composed wholly or almost wholly of cellulose.[1] The cellulose portion may be homogeneous in structure or consist of several concentric layers. In the Siphonales the innermost portion usually contains callose instead of cellulose.[2] External to the cellulose portion of a wall is a region in which pectose predominates. It is not clear whether the pectose is derived directly from the cellulose or is a secretion of the protoplast that filters through the cellulose portion. The latter appears to be the case with desmids in which there are definite pores in the wall. Cells of most genera have the outermost portion of the pectose converted into a water-soluble pectin that dissolves away in the surrounding medium. It is very probable also that the formation of pectose continues throughout the vegetative life of a cell. There are many Chlorophyceae, as the Zygnemataceae, where the amount of pectose secreted just about balances that dissolved away. The result is an equilibrium in which the thickness of the pectose layer remains practically constant.[3] If the formation of pectose ceases, as it does during conjugation in Zygnemataceae, there comes a time when the pectic layer dissolves away and there is nothing external to the cellulose portion. Not all species establish this equilibrium, and certain of them have the gelatinous portion of the wall increasing indefinitely in thickness. There are also genera where the external

[1] Tiffany, 1924; Wurdack, 1923. [2] Mirande, 1913. [3] Tiffany, 1924.

portion of the pectose becomes impregnated with chitin and where the wall is composed of three distinct portions.[1] Even if one agrees with those who deny the presence of chitin in algae,[2] it is clear that certain genera have an outermost wall layer that inhibits, or greatly reduces, dissolving away of the pectose portion. Walls of green algae may also be impregnated with lime. This is especially the case with Siphonales of tropical seas, and in them lime may accumulate in such quantity that the alga is white, not green.

The Protoplast. Most Chlorophyceae have the cytoplasm restricted to a layer next the cell wall and have a conspicuous vacuole internal to the cytoplasmic layer. Immature cells developing from zoospores have many small vacuoles scattered through the cytoplasm, and these vacuoles gradually unite to form a single central one. Sometimes, as in *Sphaeroplea* (page 66), there are several large vacuoles within a mature cell, or, as in *Spirogyra*, the central vacuole is incompletely divided by strands of cytoplasm. Vacuoles of a few species are colored because of anthocyan pigments dissolved in the cell sap. Cells of Chlorophyceae that have become adapted to a subaerial existence usually do not have central vacuoles.

Most of the Volvocales and certain of the Tetrasporales have small *contractile vacuoles*, usually two, near the base of the flagella. When two vacuoles are present, they usually contract alternately. The contraction is sudden and the distension is slow. It is thought that the contractile vacuoles are excretory organelles and that the liquid discharged from them is expelled from the cell.

The protoplast always contains one or more nuclei. Many families and orders have vegetative cells that are uninucleate except at the time of sporulation or gametogenesis. Uninucleate cells may have the nucleus embedded in the peripheral layer of cytoplasm or suspended in the central vacuole by cytoplasmic strands connected with the peripheral cytoplasm. Multinucleate vegetative cells (*coenocytes*) are found both among Chlorophyceae which do not have vegetative cell division and among those whose cells divide vegetatively. Most coenocytes have a gradual increase in number of nuclei as a cell increases in size. Nuclei of both uni- and multinucleate cells have a distinct nuclear membrane, one or more nucleoli, and a chromatin-linin network. The amount of chromatin is often so scanty that the space between nucleolus and membrane is almost colorless. Nuclear division is mitotic and similar to that in vascular plants.

The chloroplast is the most conspicuous organelle of the protoplast. The amount of pigmentation of chloroplasts is extremely variable and ranges all the way from a quantity sufficient to color the plastid a brilliant

[1] Wurdack, 1923. [2] Wettstein, von, 1921.

green to an amount so small that there is only a tinge of color. A few Chlorophyceae completely lack photosynthetic pigments. Most Chlorophyceae have no other pigmentation than chlorophyll and its associated pigments. A few species, including *Trentepohlia* (page 54), have the green color completely masked by an orange-red pigment (*haematochrome*) that is thought to be of a carotinoid nature. The function of the haematochrome of *Trentepohlia* is uncertain, but its accumulation in recently formed cells has been held[1] as proof that it functions as a food reserve rather than as a light screen.

Chloroplasts always have a shape characteristic for the particular species, and this is often characteristic of the genus and family. Old cells of many species seem to have the chlorophyll diffused throughout the cytoplasm, but young cells of all of them have definite chloroplasts. The shape of the chloroplast is extremely varied when the Chlorophyceae are taken as a whole. The massive cup-shaped chloroplast found in most species of *Chlamydomonas* is also found in many other Volvocales and in Tetrasporales. This widespread occurrence of cup-shaped chloroplasts among the lower Chlorophyceae gives good reason for supposing that it is the primitive type. In more advanced green algae, as the Ulotrichales, the chloroplast is parietal in position, laminate, and entire or perforate. Cells of a considerable number of genera, especially those belonging to the Siphonales, have numerous small discoform chloroplasts at the periphery of the protoplast. The most striking of all chloroplasts are found in the desmids, and the range in shape from genus to genus is almost infinite.

Most chloroplasts contain a special organelle, the *pyrenoid*. Structurally, the pyrenoid consists of a central core, of a proteinaceous nature, ensheathed by plates of starch (Fig 2). Strictly speaking, the term pyrenoid should be applied only to the central protein portion, but in common usage it is often applied to both the protein portion and to the surrounding starch plates. With a few exceptions all present-day phycologists hold that the protein portion is intimately concerned with the formation of the starch plates. According to one interpretation,[2] the body of a pyrenoid becomes differentiated into two parts: one destined to be transformed into a starch plate; the other to remain unchanged. The part undergoing change gradually gives more and more of a starch reaction, moves away from the unchanged part, and eventually becomes one of the starch plates surrounding the pyrenoid. According to another interpretation,[3] starch grains are at first minute granules external to the pyrenoid; later on they increase in size by deposition of starch on all sides. Small chloroplasts usually contain a single pyrenoid; large chloroplasts usually contain several of them. In chloroplasts of certain species

[1] Geitler, 1923. [2] Timberlake, 1901. [3] Czurda, 1928.

it is quite clear that pyrenoids are formed by division of a preexisting pyrenoid; in other species it is equally clear that they are formed *de novo*.

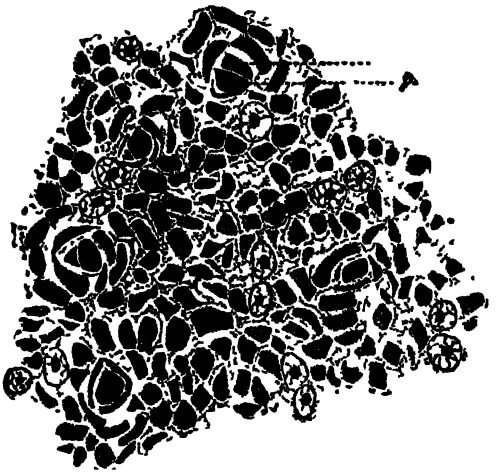


FIG. 2.—Pyrenoids of *Hydrodictyon*, showing the cutting off of starch plates (*From Timberlake*, 1901)

Chloroplasts in cells of certain species regularly lack pyrenoids. Most of these species, in spite of their lack of pyrenoids, regularly form starch.

Chlorophyceae also store reserve foods as fats. The oil droplets so frequently present in zygotes and in old vegetative cells are probably conversion products from starch. On the other hand, there are some green algae whose vegetative cells form only fats. The most notable of these is *Vaucheria*, but it is interesting to note that even this alga sometimes forms starch when constantly illuminated.[1]

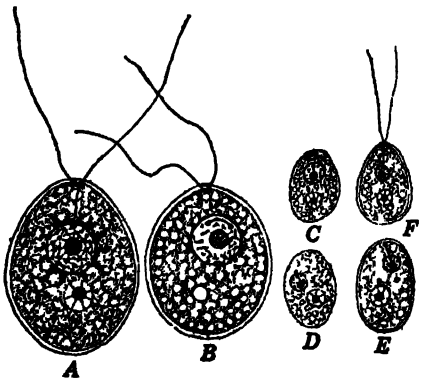


FIG. 3.—Neuromotor apparatus of *Chlamydomonas nasuta* Korshikov. *A*, neuromotor apparatus of a vegetative cell. *B*, at the beginning of cell division. *C–F*, development of the neuromotor apparatus in a young cell. (*All after Kater*, 1929.) (× 1284.)

Flagella and Eyespots. Motile vegetative and reproductive cells (*zooids*) of Chlorophyceae are propelled through the water by special organelles, the *flagella*, that are inserted (borne) at the anterior end of the cell. Most zooids have two flagella, but there may be four, eight, or many of them. In all but a few exceptional cases the flagella of a zooid are of equal length.

Flagella of vegetative cells, and probably also those of zoospores and gametes, are produced by the *neuromotor apparatus*, an organelle inti-

[1] Tiffany, 1924.

mately associated with the nucleus. The neuromotor apparatus of *Chlamydomonas nasuta* Korshikov is of an elaborate type[1] and more or less similar ones have been found[2] in several other Volvocales. There is, first of all, a granule (*blepharoplast*) at the base of each flagellum (Fig. 3). The blepharoplasts are connected with each other by a transverse fiber (the *paradesmose*), and it is connected to a small intranuclear *centrosome* by another delicate fiber (the *rhizoplast*). The centrosome, in turn, is connected with the nucleolus by a delicate fibril, but this is probably without significance.

All parts of the neuromotor apparatus except the centrosome disappear at the beginning of cell division in *Chlamydomonas nasuta*. The centrosome then divides into two daughter centrosomes which come to lie at opposite poles of the intranuclear spindle. When daughter nuclei are reorganized from the divided chromosomes, there is a single centrosome within each nucleus. The formation of a new neuromotor apparatus begins with an elongation of the centrosome into a dumbbell-shaped structure, one end of which projects through the nuclear membrane. This free end, the blepharoplast, eventually migrates to the anterior end of the cell, spinning out a rhizoplast between it and the end remaining within the nucleus, the intranuclear centrosome. The blepharoplast divides into two daughter blepharoplasts after reaching the anterior end of the cell, and they remain connected with each other by a paradesmose. The method by which each daughter blepharoplast causes the development of a flagellum is uncertain.

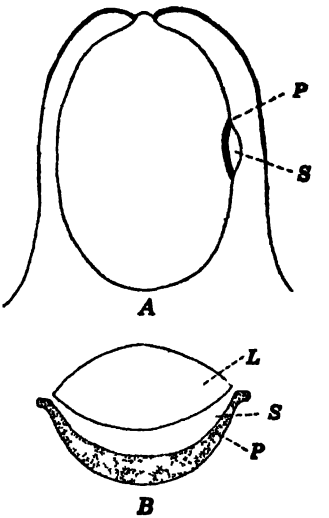


FIG. 4.—*A*, diagram of an eyespot of *Chlamydomonas* showing the pigment cup *P* and the photosensitive substance *S*. *B*, diagram of a cross section of the eyespot of *Volvox*, through the lens *L*, photosensitive substance *S*, and the pigment cup *P*. (*Modified from Mast*, 1928.)

The flagella of green algae are not homogeneous in structure but consist[3] of a distinct axial filament surrounded for the greater part of their length by a cytoplasmic sheath. The cytoplasmic sheath usually ends abruptly; the naked portion of the axial filament extending beyond it is known as the *endpiece*.

Zooids usually have an *eyespot* or *stigma*. An eyespot is orange-red to reddish brown, and it may be circular, oval, or sublinear in outline.

[1] Kater, 1929.
[2] Entz, 1918; Hartmann, 1921; Kater, 1925; Zimmermann, 1921.
[3] Petersen, 1929.

It is usually located near the base of the flagella, but it may lie in the equator of a cell. Division of protoplasts of Volvocales may be accompanied by a bipartition of the eyespot, or new eyespots may be formed *de novo* in each daughter protoplast. Nonflagellated vegetative cells of the higher green algae do not have eyespots. An eyespot may appear just before zoospore or gamete formation and be divided each time the protoplast divides, or eyespots may not appear until all divisions of the protoplast have been completed.

The eyespot is a photoreceptive organelle intimately concerned with directing movement of the flagella. Possibly it is a part of the neuromotor system, as has been claimed,[1] but as yet there has been no cytological demonstration of the fact. In *Chlamydomonas* (Fig. 4*A*) and possibly other unicellular Volvocales, the eyespot consists of two portions; a biconvex hyaline portion, which is the photoreceptive part, and a curved pigmented plate.[1] *Volvox* and certain other colonial genera have a more complicated type of eyespot (Fig 4*B*). Here there is a definite biconvex lens, a curved colorless photosensitive portion, and a curved pigmented portion.[2] Phototactic responses in Volvocales with this type of eyespot are thought to be due to selective reflection from the concave surface of the pigmented portion.

Cell Division. Cells of all Chlorophyceae except those of Chlorococcales and Siphonales divide vegetatively Division is intercalary in most unbranched filamentous genera, and, except for the basal cell, any cell of a filament may divide Division is also intercalary in branching filamentous genera, but in most cases the divisions are restricted to terminal portions of the branches, although not necessarily to the apical cells. In most nonfilamentous colonial genera there may be a division of any cell in the colony.

Cytokinesis of uninucleate cells is always preceded by a mitotic division of the nucleus; coenocytic cells may or may not have nuclear divisions preceding cell division. The usual method of cell division is by a furrowing of the plasma membrane midway between the cell ends. This linear furrow deepens until it has cut entirely through the protoplast and formed two daughter protoplasts. There is great variability in the time at which new transverse walls are formed and in the method of their formation. Most cells secrete wall material within the furrow as it deepens. In fact, cross-wall formation follows so closely upon furrowing that cell division is often thought to be caused by an inward growth of a transverse septum. Sometimes, as in *Oedogonium*, division of the protoplast is completed before the beginning of cross-wall formation (page 70). In a few Chlorophyceae[3] cell division is by means of a cell plate (*phragmoplast*) as in cells of vascular plants.

[1] Mast. 1928. [2] Mast, 1916, 1928. [3] McAllister, 1913; 1931; Mainx, 1927.

Division of the protoplast may be accompanied by division of the chloroplast. The chloroplast may be divided transversely (*Spirogyra, Ulothrix*), or longitudinally (*Chlamydomonas*). Uninucleate cells with a chloroplast axial to either pole of the nucleus, as *Zygnema*, have division of the chloroplast taking place after cytokinesis.

Many Chlorophyceae show a marked diurnal periodicity in the time at which nuclear and cell division take place. In the great majority of cases it is at night. Nuclear division usually begins within an hour or two after sundown and is often completed shortly after midnight. Cell division usually takes place during the early morning hours. It is not improbable that this diurnal periodicity is correlated with accumulation of reserve foods following the photosynthetic activity of the daytime.

Asexual Reproduction. Asexual reproduction of colonial genera may be vegetative and by a fragmentation of the colony. Fragmentation of filamentous genera may be purely accidental, or it may be due to a formation of spores or gametes here and there along a filament. Under certain environmental conditions, some genera have a regular dissociation into individual cells or short files of a few cells each. Such fragments may subsequently grow into long filaments. Nonfilamentous colonies may reproduce vegetatively by an accidental fragmentation or by an abscission of proliferous outgrowths.

Asexual reproduction may also be due to the formation of one or more spores within a cell All cells producing spores are *sporangia,* but among the Chlorophyceae it is customary to apply this term only to those genera, as *Trentepohlia*, where the sporangia are morphologically different from vegetative cells. The spores may be naked and motile (Fig. 16*B*) or nonmotile and surrounded by a wall. Motile spores (*zoospores*, Fig. 16*B*) have two, four, or more flagella at the anterior end. If a nonmotile spore has a wall distinct from the parent-cell wall, it is an *aplanospore*[1] (Fig. 16*C*). Aplanospores with greatly thickened walls are usually called *hypnospores*. Nonmotile spores formed singly within a cell may have a wall that is not distinct from the parent-cell wall. Such spores are *akinetes* (Fig. 31*G*). Vegetative cells may also develop directly into akinetes with greatly thickened walls and abundant food reserves. Such akinetes are to be interpreted as vegetative cells better adapted to tide the alga over unfavorable conditions.

Aplanospores are in reality modified zoospores that have secreted a wall before liberation from the sporangial cell. The type of spore produced by a green alga is frequently dependent upon environmental conditions; thus, as in *Vaucheria*, it is not uncommon to find the same species producing zoospores when it grows submerged in water and producing aplanospores when it grows in subaerial habitats.

[1] Wille, 1883.

Zoospore formation, like cell division, frequently takes place at night, and the spores are usually liberated at daybreak. Sudden changes in the environment often stimulate profuse sporulation, and it is no unusual experience to find many algae producing zoospores the day after they are brought into the laboratory. For certain algae this has been shown[1] to be due to an increase in the amount of carbon dioxide in the water.

Some genera produce a single zoospore within a cell, but most genera have each cell producing more than one. The number of zoospores formed by a uninucleate cell is a multiple of 2 and usually 4, 8, or 16. This is due either to successive simultaneous nuclear divisions before cleavage into uninucleate protoplasts or to simultaneous successive bipartitions of the protoplast. Coenocytic cells also have a cleavage into uninucleate protoplasts, but their number is not necessarily a multiple of two. Cleavage of cells with several nuclei may be *simultaneous;* or *progressive*, and into masses with smaller and smaller numbers of nuclei (Fig. 48*C–D*). Irrespective of whether formed by simultaneous or progressive cleavage, the uninucleate protoplasts are then metamorphosed into zoospores with a specific number of flagella. Blepharoplasts have been observed[2] in developing zoospores of several species, and at least one genus is known[3] to have a definite neuromotor apparatus Zoospores resemble vegetative cells of unicellular Volvocales, and from the phylogenetic standpoint they may be looked upon as a temporary reversion to the primitive ancestral flagellated condition.

Liberation of zoospores is generally through a pore in the surrounding wall, but it may also be effected by a breaking or gelatinization of the wall Zoospores of most genera swim freely in all directions after liberation, but in many cases the direction in which they swim is influenced by external stimuli, especially light and gravity. The duration of swarming is dependent upon the particular species and upon environmental conditions. The normal swarming period generally lasts from 30 minutes to 2 hours, but it may be as short as 3 or 4 minutes (*Pediastrum*)[4] or as long as 2 or 3 days (*Ulothrix*).[5] Movement becomes more and more sluggish toward the end of the swarming period, and a slow lashing of the flagella often continues after zoospores have come to rest Shortly after ceasing to swarm, the zoospore retracts or loses its flagella and secretes a wall. These one-celled plants are usually sessile and are attached to the substratum by means of pectose material in the newly formed wall. Colonial species soon have the one-celled stage developing into a many-celled colony.

[1] Gussewa, 1927, 1930; Uspenskaja, 1930
[2] Davis, 1908; Gussewa, 1930; Timberlake, 1902. [3] Reich, 1926.
[4] Harper, 1918 [5] Klebs, 1896.

Aplanospores may be liberated by a breaking of the mother-cell wall or only after its decay. They may germinate directly into new plants, or they may produce zoospores that develop into new plants.

Sexual Reproduction. The Chlorophyceae are an evolutionary series in which gametic union became firmly established in the most primitive forms and persists among the highest members of the series. Gametic union of many species is *isogamous* (Fig. 8*B*) and with a fusion of two flagellated or nonflagellated gametes of equal size. Other species are either *anisogamous* (Fig. 9*E*) and with a union of two flagellated gametes of unequal size or *oogamous* (Fig. 13*B*) and with a small motile male gamete (*antherozoid*) uniting with a large immobile gamete (*egg*). In at least four independent lines among the green algae, there has been an evolution from isogamy to oogamy.

Many Chlorophyceae show a marked seasonal periodicity in the occurrence of their sexual reproduction. In fresh-water algae this usually takes place late in the spring, but it may not take place until the fall. Sexual reproduction of *Spirogyra* seems to take place only when a certain amount of reserve food has accumulated. Here, the accumulation of a sufficient food reserve is directly dependent upon the ratio between surface of cell, volume of the cell, and the temperature [1] The prevalent idea that a lowering of the water supply in a pool induces fruiting is incorrect, since it has been shown[2] that there is an even more abundant fruiting if weather conditions are such that the water level of a pool does not fall

The production of flagellated gametes (*zoogametes*) is almost identical with that of zoospores Gamete-producing cells, the *gametangia*, are generally morphologically indistinguishable from vegetative cells.

All green algae in which both gametes are nonflagellated (*aplanogamous*) are isogamous Aplanogamy is found throughout the Zygnematales and is a feature immediately separating them from other Chlorophyceae. Some Zygnematales are truly isogamous and with both gametes of a uniting pair amoeboid Other Zygnematales, as *Spirogyra*, have the morphological isogamy accompanied by a physiological differentiation in which one gamete is passive and the other actively amoeboid.

In anisogamous species the larger gamete of the two is always considered the female. It may be but little larger than the male gamete (*Pandorina*, page 33), or it may be many times larger (*Codium*, page 113).

With one exception (*Sphaeroplea*, page 66), eggs of oögamous species are produced singly within a gametangium, the *oögonium*, morphologically different from vegetative cells. The *antheridium*, the game-

[1] Transeau, 1916. [2] Transeau, 1913

tangium producing the antherozoids, is also generally of a distinctive form, and it usually produces more than one antherozoid.

Both of a uniting pair of iso- or anisogamous gametes may be actively motile at the time of gametic union, or one may be motile and the other immobile. Almost all of the oogamous Chlorophyceae have a swimming of the antherozoid into the oögonium and gametic union taking place there.

Iso-, aniso-, and oogamous species may be *homothallic* and with a union of gametes from the same cell or thallus; or they may be *heterothallic* and only have a union of gametes when the two come from cells of different parentage. Certain heterothallic algae have a genotypic differentiation into the two kinds of thalli at the time of zygote germination.[1]

There are numerous records of cases where gametes that have not united with one another have developed into new plants or into resting stages identical in appearance with zygotes. The evaluation of these records of *parthenogenesis* is a difficult matter since they have been observed in mixed cultures. However, pure cultures have demonstrated that gametes of some species develop parthenogenetically,[2] and those of others do not.[3] The development of gametes into zygote-like bodies (*parthenospores*) is a well-established fact among the Zygnematales.

The Zygote and Its Germination. Zoogametes may not have a disappearance of the flagella when they unite in pairs, and the resultant zygote may swarm in much the same fashion as a zoospore before it comes to rest and secretes a wall. All zygotes of oogamous Chlorophyceae are, of course, immobile from the beginning, and they all secrete a wall within a fairly short time. The zygote wall is a thin homogeneous structure when first formed, but later on it often becomes differentiated into three layers, the outer two of which contain cellulose. Zygotes of many species have a characteristic ornamentation and coloration. Among species with a zygote entering upon a resting period, the young zygotes are a bright green and contain such food reserves as were present in the gametes. Photosynthesis by the ripening zygote may result in an accumulation of still more food. At first the food reserves consist almost wholly of starch; later on there is often a conversion of the starch into fats. There is often, also, a development of haematochrome in sufficient quantity to color the protoplast a bright red or an orange-red.

Sooner or later the two nuclei contributed by the two gametes fuse with each other. The fate of the chloroplasts is harder to follow. In the case of *Zygnema*[4] and certain desmids[5] the chloroplasts derived from the female gamete persist, and those contributed by the male gamete degenerate.

[1] Schreiber, 1925; Mainx, 1931 [2] Schulze, 1927 [3] Hollenberg, 1935.
[4] Kurssanow, 1911 [5] Potthoff, 1927.

Many, if not all, of the Volvocales, Ulotrichales, Oedogoniales, and Zygnematales have a reductional division of the zygote nucleus. It seems equally certain that division of the zygote nucleus is equational, not reductional, in certain Cladophorales, Ulvales, and Siphonales.

Zygotes with the nucleus dividing reductionally do not germinate immediately. The time interval for ripening is often a matter of months, and it has been shown that zygotes of *Ulothrix* germinate 5 to 9 months after they are formed[1] and that those of *Oedogonium* have a resting period of 12 to 14 months.[2] In most cases meiosis results in four nuclei, but there are cases where one of the daughter nuclei of the first division degenerates and the other divides into two nuclei. All resting zygotes but those of Zygnematales have meiosis followed by a formation of zoospores. There is usually a division into four zoospores at the quadrinucleate stage, but a germinating zygote may also give rise to more or less than four zoospores; the production of less than four nuclei is due to a degeneration of one or more of them; the production of more than four, as in *Coleochaete* (page 53) is due to further nuclear divisions after meiosis.

Zygnematales do not form zoospores when a zygote germinates. Some genera have a persistence of all four nuclei after meiosis and a division into four uninucleate protoplasts, each of which develops directly into a new plant. Other genera either have two of the four nuclei nonfunctional and a formation of two germlings, or a degeneration of three nuclei and a production of but one new plant.

Zygotes with the nucleus dividing equationally usually germinate within two or three days after gametic union. Division of the daughter nuclei is also equational, and meiosis does not take place until just before reproduction. Depending upon the species, this may be sporogenesis or gametogenesis.

Life Cycle of Chlorophyceae. Unicellular Volvocales reproducing sexually have the simplest possible type of a life cycle (Fig. 5*A*). Here cell division results in the formation of two, four, or eight motile daughter cells which are strictly homologous with the zoospores of other Chlorophyceae. From the morphological standpoint, these one-celled plants produce zoospores which, in turn, metamorphose into motile one-celled plants. The vegetative cells may also give rise to zoogametes that fuse in pairs to form a zygote. The nucleus of a germinating zygote divides meiotically, and there is a production of four zoospores which function directly as one-celled vegetative plants. The life cycle of these primitive algae consists, therefore, of an alternation of a one-celled haploid phase with a one-celled diploid phase. Such alternation is not obligatory in the sense that the haploid phase must always give rise to the diploid phase

[1] Gross, 1931 [2] Mainx, 1931.

since there may be a succession of haploid phases before production of a diploid phase. The alternation is, however, obligatory in the sense that the diploid phase cannot give rise to further diploid phases but must always form the haploid phase.

This primitive cycle may have been succeeded by one with vegetative cell division in either phase. The great majority of Chlorophyceae have had an interpolation of vegetative cell division in the haploid phase (Fig. 5*B*). This results, as in *Oedogonium*, in a life cycle with a multi-

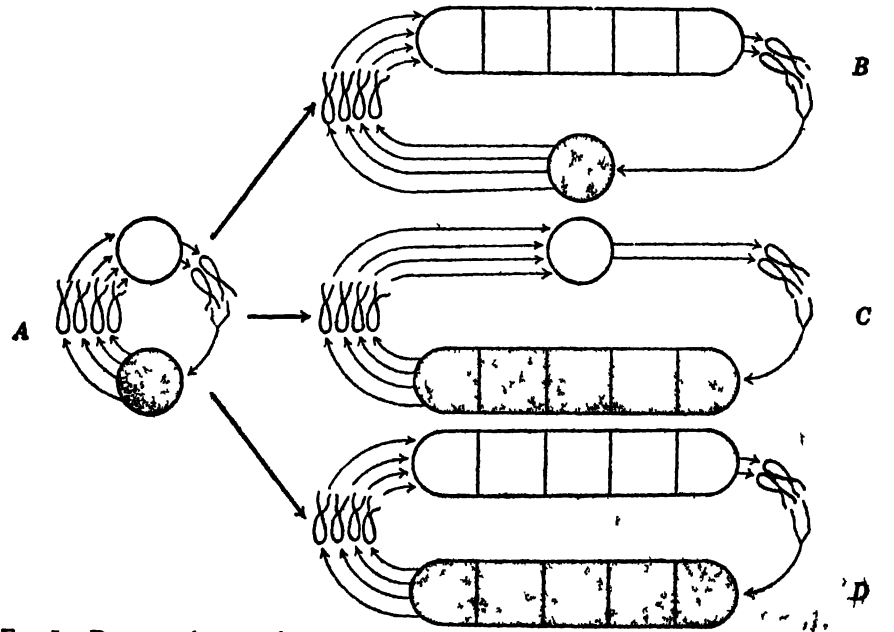


Fig. 5.—Diagram showing the various types of life cycle among the Chlorophyceae *A*, chlamydomonad *B*, haplontic *C*, diplontic *D*, Diplohaplontic

cellular haploid generation alternating with a unicellular diploid phase Such *haplonts*[1] usually have the haploid generation reproducing asexually by means of zoospores or modifications of zoospores *Codium* and *Bryopsis* represent instances where there has been an interpolation of vegetative division in the diploid side of the cycle (Fig 5*C*). In these *diplonts* the life cycle consists of an alternation of a diploid coenocyte, the morphological equivalent of a multicellular diploid generation, with a unicellular haploid phase.

Certain Ulvaceae and Cladophoraceae are known to be *diplohaplonts*[1] and to have a life cycle in which there is an alternation of a many-celled haploid generation with a many-celled diploid generation (Fig 5*D*) The alternating generations of Ulvaceae and Cladophoraceae are identical

[1] Svedelius, 1931.

in appearance and cannot be distinguished from each other until the time of reproduction. In some species the alternation is strictly obligate; in others there may be a reduplication of the haploid generation by a parthenogenetic germination of zoogametes. Diplohaplonts with similar gametophytic and sporophytic generations probably arose from a haplont through a failure of meiosis in the germinating zygote. Since each of the two haploid gametes forming the zygote had contributed an identical set of genes for size and shape of plant body, the diploid zygote grew into a multicellular thallus identical in form with the haploid thallus. In Ulvaceae and Cladophoraceae the capacity for meiosis, originally present in the zygote, is transmitted through each cell generation of the diploid plant. Nuclei in cells of diploid plants usually do not divide reductionally until the plant is fully mature, but meiosis may take place while the diploid plant is still juvenile. Nuclei of all cells of the diploid generation may divide meiotically, as in *Ulva*, or meiosis may be restricted to young, actively growing cells at branch tips, as in *Cladophora*.

The two alternating generations in a diplohaplonic life cycle may be dissimilar instead of identical. One green alga, *Urospora*, has been shown[1] to be of this type. Here there is an alternation of a filamentous many-celled haploid generation with a coenocytic diploid generation. *Urospora* seems to have been evolved from a haplontic ancestor. However, it is equally possible for this diplohaplontic life cycle with dissimilar generations to have arisen from a primitive life cycle where there are alternating haploid and diploid one-celled phases.

Evolution in the Chlorophyceae. The major sweep in evolution of Chlorophyceae from a one-celled flagellated condition has been in construction of the plant body, rather than in an evolution from isogamy to oögamy or an evolution of an alternation of generations. This was first recognized when Blackman[2] postulated his theory of vegetative tendencies. According to this theory, evolution from a unicellular flagellated condition took place along three main evolutionary lines or tendencies. These are: (1) the *volvocine tendency* in which the cells divide vegetatively, but in which the daughter cells retain their motility when organized into a colony; (2) the *tetrasporine tendency* in which there is a loss of motility, except in reproductive stages, but in which there is a development of colonies by vegetative division; (3) the *chlorococcine* (*endosporine*) *tendency* in which there is a loss of motility, except at the time of reproduction, and no capacity to divide vegetatively. To these should be added (4) the *rhizopodal tendency* in which there is an evolution toward a naked amoeboid type of organization.

[1] Jorde, 1933. [2] Blackman, 1900.

Evolution of the green algae has been along the first three of the above tendencies (Fig. 6). The evolutionary possibilities along the volvocine line are extremely limited since a colony cannot be of any appreciable size and still have all the cells motile. There are several motile colonial Volvocales, and *Volvox*, the culminating member of the series, probably approaches the limit of evolution along this line.

Evolution along the chlorococcine line has been in several directions. Some of the Chlorococcales show an evolutionary advance from a uninucleate to a coenocytic condition. Others of them show an evolution

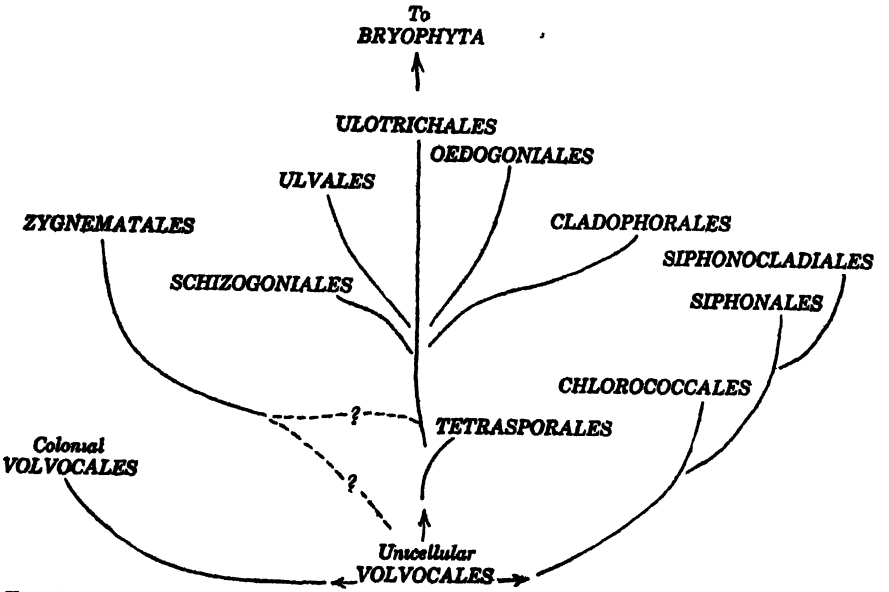


FIG. 6—Diagram showing the suggested interrelationships among the Chlorophyceae

of the colonial habit resulting from an apposition of zoospores or aplanospores. However, these colonial genera never have an increase in number of cells once a colony is formed. The unicellular coenocytic forms with limited growth of the coenocyte lead to those in which growth is more or less unlimited. From such simple siphonaceous forms, as *Protosiphon* (page 95), it is not a great step to the more elaborate Siphonales. The Siphonocladiales, an offshoot from the Siphonales, are unicellular coenocytes in which the cell has become multicellular by transverse septation.

The evolutionary possibilities along the tetrasporine line are infinite. A tendency for the vegetative cells to become nonflagellated but to return directly to the motile condition is found in the temporary *Palmella* stages of many unicellular Volvocales, including *Chlamydomonas*. It is but a small step from them to the truly palmelloid Tetrasporales where

the immobile vegetative cell is the dominant phase and where the vegetative cells are only temporarily motile. Protoplasts of Tetrasporales have a marked tendency to divide into fours and eights and for the daughter cells thus formed to become separated from one another by a secretion of gelatinous materials. Restriction of cell division to a bipartition and the restriction of all divisions to the same plane would result in the filamentous organization characteristic of the Ulotrichales. Evolution of the Ulotrichales was accompanied by another feature, a loss of the ability of the protoplast to return directly to a motile condition; and there are no filamentous Chlorophyceae with this feature so characteristic of Tetrasporales. An appearance of the ability to divide both vertically and transversely lead to the Ulvales, an order that seems to be an offshoot from the Ulotrichales, in which the plant body is a sheet, a hollow sac, or a solid cylinder. Other Chlorophyceae evolved from the ulotrichaceous type differ in structure of their protoplasts or of their spores or gametes rather than in their body construction. In one line, the Cladophorales, there was an evolution of a coenocytic condition in each cell of the filament. In other lines, segregated as separate orders by systematists, there was an evolution of a distinctive type of zooid (Oedogoniales) or an evolution of distinctive aplanogametes (Zygnematales).

The Byrophyta probably originated among the branching filamentous ulotrichaeous Chlorophyceae, but the steps in their evolution are wholly a matter of conjecture since there is a very long gap between the most complex of branching Ulotrichales and the simplest bryophytes.

Classification. Phycologists are in general agreement concerning the natural affinities of many groups of genera (variously included in the Volvocaceae, Hydrodictyaceae, Ulvaceae, Cladophoraceae, Oedogoniaceae, Zygnemataceae, and Desmidiaceae), but there is great diversity of opinion concerning the limits of groups larger than the family.

The Chlorophyceae are here divided into eleven orders, five of which (Volvocales, Ulotrichales, Zygnematales, Chlorococcales, and Siphonales) are universally recognized by phycologists. Because the limits between the two are obscure, opinion is about equally divided as to whether the Tetrasporales should be a separate order or included with the Volvocales. There is also disagreement concerning the limits of the Ulotrichales. Some consider the Ulvales a family of the Ulotrichales; others remove the Chaetophoraceae and certain other families with branching filaments from the Ulotrichales and place them in a separate order. The Siphonocladiales are also controversial, and, as will be noted later (page 122), their validity has even been questioned. Almost all present-day phycologists have abandoned the former practice of placing the Zygnematales in a special subclass.

ORDER 1. VOLVOCALES

The Volvocales are the only Chlorophyceae in which the vegetative cells are flagellated and actively motile. The cells may be solitary or united in colonies of definite form and with a definite number of cells. Asexual reproduction is by the formation of zoospores or by the formation of motile daughter colonies. Most genera reproduce sexually, and gametic union ranges from isogamy to oogamy.

There are more than 50 genera and 325 species of Volvocales. Almost all of them are fresh-water in habit, and frequently they develop luxuriantly in waters rich in soluble nitrogenous compounds.

Most genera have cells that are ovoid, cordiform, or fusiform, but some have cells that are compressed or with an irregular outline. Some genera have naked protoplasts, but most of them have cells with a definite wall with a cellulose layer next to the protoplast. Frequently there is a layer of pectic material external to the cellulose, and in colonial genera the individual envelopes may be completely fused with one another to form a homogeneous colonial matrix. Walls of a few unicellular genera consist of two overlapping halves that separate from each other at the time of reproduction.

The general organization of the protoplast throughout the order is more or less like that of *Chlamydomonas*. However, the amount of pigmentation in the chloroplast is extremely variable, and there are genera in which there is but a trace of chlorophyll or in which there is no chlorophyll. The lack of chlorophyll does not exclude such saphrophytic genera from the Volvocales, since other features of cell structure are typical for the order, including the presence of a pyrenoid and a regular formation of starch.

Asexual reproduction of unicellular genera whose cells are not enclosed by a wall is by a longitudinal division into two daughter cells, and cleavage may begin at the posterior or at the anterior end. Unicellular genera with a cell wall have a division of the protoplast into two, four, or eight daughter cells which are the morphological equivalent of zoospores Colonial genera may have all or only certain cells dividing and redividing to form daughter colonies.

Sexual reproduction is isogamous, anisogamous, or oögamous. In iso- and anisogamous gametic union both of a uniting pair of gametes are usually free-swimming. In oogamous gametic union the egg generally remains within the wall of the cell producing it.

The Volvocales are generally divided into five or six families. Of the families discussed below, one is representative of those whose cells are solitary; the other is representative of those whose cells are united in colonies.

FAMILY 1. CHLAMYDOMONADACEAE

The Chlamydomonadaceae include all of the unicellular Volvocales with a definite wall except those with a wall composed of two overlapping halves or those with a protoplast containing numerous contractile vacuoles. The cells may be bi- or quadriflagellate. Asexual reproduction is by a division into zoospores that secrete a wall of their own and develop flagella before liberation by rupture or gelatinization of the parent-cell wall Gametic union is usually isogamous, but a few species are anisogamous and one[1] is known to be oogamous.

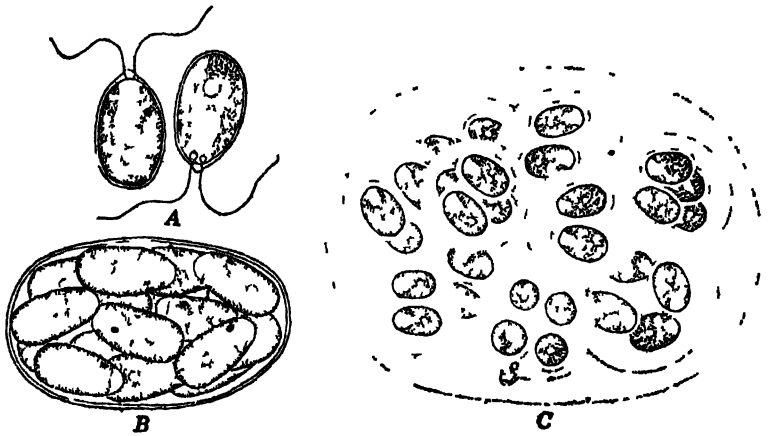


FIG. 7.—*A B Chlamydomonas Snowiae* Printz *A*, vegetative cells. *B*, gamete formation *C*, *Palmella* stage of an undetermined *Chlamydomonas* species (× 1000)

The family contains about 27 genera and 250 species, almost all of them fresh-water

Chlamydomonas, with some 150 species, is a widely distributed fresh-water organism in standing water and on moist soil. It often grows in abundance in water rich in ammonium compounds, as pools in barnyards.

The cells (Fig 7*A*) are biflagellate and spherical, ellipsoidal, subcylindrical, or pyriform. The two flagella are anterior in insertion, fairly close together, and the contour of the cell may or may not be distinctly papillate in the region bearing the flagella. There is always a definite cellulose wall, and some species have a gelatinous sheath external to the cellulose layer. Most species have a single cup-shaped chloroplast. Chloroplasts of this type may be massive and occupy most of the protoplast, or the flanks of the cup may be relatively thin. Other species have chloroplasts that are either laminate, stellate, or H-shaped in optical section.[2] Chloroplasts of most species contain a single pyrenoid, but those of certain species contain two pyrenoids, several parietal pyrenoids,

[1] Pascher, 1931. [2] Pascher, 1927.

or no pyrenoids at all. Typically there are two contractile vacuoles near the base of the flagella, but the number and position of vacuoles are not constant for the genus. The shape and position of the eyespot are fairly constant for any given species, but, taking the genus as a whole, the eyespot may lie anywhere between insertion of the flagella and the lower third of a cell. It may be circular, oval, or sublinear in outline. All species are uninucleate. Species with a cup-shaped chloroplast have the nucleus lying in the colorless cytoplasm filling the cup; other species may have the nucleus axial and midway between the two poles, or axially excentric.

Asexual reproduction is by division of the protoplast into two, four, or eight daughter protoplasts that secrete a wall and develop flagella before liberation from the parent-cell wall. The number of daughter cells, the morphological equivalent of zoospores, is partially dependent upon the physiological condition of the parent cell. Cells growing under favorable conditions usually form a larger number of daughter cells than do those whose environment is less favorable. Dividing cells are usually immobile, but their flagella may not be retracted or discarded. Reproduction begins with a longitudinal division of the protoplast into two daughter protoplasts; this is usually followed by a simultaneous division of each daughter protoplast and sometimes by a third series of divisions. After division has been completed, each daughter protoplast secretes a wall of its own and develops a neuromotor apparatus that forms two flagella (page 16). Daughter cells are liberated by a gelatinization or by a rupture of the parent-cell wall. In rare cases[1] the protoplast of a vegetative cell may round up and develop into an aplanospore.

Under certain conditions, as when growing on damp soil, the daughter cells do not develop flagella and become motile but remain embedded within a matrix formed by gelatinization of the parent-cell wall. Division and redivision of the daughter cells may produce an amorphous colony with hundreds or thousands of cells, all embedded within a common gelatinous matrix. Such *Palmella* stages (Fig. 7*C*), so-called because the older phycologists thought them to be species of *Palmella*, may have the cells developing flagella and swimming away. Cells of terrestrial *Palmella* stages frequently do this when flooded, and it is not unusual to find all cells of a colony swimming freely in all directions a few minutes after flooding. Sometimes cells of *Palmella* stages develop into thick-walled akinetes (hypnospores).

At the time of sexual reproduction the protoplast of a cell divides into 8, 16, or 32 biflagellate gametes (Fig. 7*B*). The gametes may be naked or surrounded by a wall. In the latter case the walls may be left behind as the gametes fuse in pairs,[2] or they may be retained.[3] Some species

[1] Wille, 1903 [2] Klebs, 1896; Pascher, 1916. [3] Moewus, 1933.

are homothallic. Others are heterothallic,[1] and certain of them have been shown[2] to have a genotypic differentiation of sex at the time of zygote germination. A fusing pair of gametes (Fig. 8*A–B*) are usually of equal size, but anisogamy has been reported[3] for a couple of species. Both gametes may be actively motile at the time of gametic union, or one may be motile and the other immobile. In the latter case there may be a clumping of many motile gametes about a single immobile one.[4] The flagella may disappear during gametic union, or they may persist (Fig.

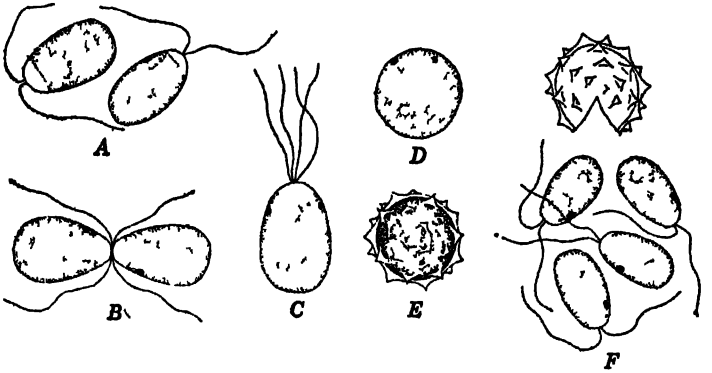


FIG. 8.—*Chlamydomonas* sp. *A*, gametes. *B*, gametic union. *C*, *D*, young zygotes. *E*, mature zygote. *F*, germination of zygote. (All diagrammatic.) (× 1,000.)

8*C*), and the quadriflagellate zygote may remain motile for as many as 15 days[5] before coming to rest and secreting a wall.

A resting zygote has a thick wall that often has a stellate or a reticulate ornamentation (Fig. 8*E*). Many ripening zygotes have haematochrome masking the chlorophyll and also a conversion of the reserve starch into fats. Prior to germination there is a reduction division of the zygote nucleus.[6] Typically, four nuclei are formed as a result of meiosis, but the number may be smaller because of nuclear degeneration after the first or the second division. Meiosis is followed by a cleavage into uninucleate protoplasts and a metamorphosis of them into biflagellate zoospores that are liberated by a rupture of the zygote wall (Fig. 8*F*).

FAMILY 2. VOLVOCACEAE

The Volvocaceae include all the motile genera in which the cells lie in a disk or a hollow sphere and not in superimposed tiers. The number of cells in a colony is definite, a multiple of two, and there is no increase in number of cells after the juvenile phases of development. In asexual reproduction all or certain cells of a colony divide simultaneously to form daughter colonies. Sexual reproduction is isogamous,

[1] Moewus, 1933, 1936; Strehlow, 1929.
[2] Moewus, 1933, 1936.
[3] Goroschankin, 1890, 1905.
[4] Moewus, 1933; Pascher, 1931*A*.
[5] Strehlow, 1929.
[6] Moewus, 1936.

anisogamous, or oögamous. All or only certain cells of a colony may be gametogenic.

The family includes some 8 genera and 25 species, all of them freshwater.

Vegetative cells are always biflagellate and almost always with a structure similar to that of *Chlamydomonas*. Cells of all genera have a gelatinous sheath, and the abutting sheaths may be distinct from one another or confluent to form a homogeneous colonial matrix. One genus (*Volvox*) has fairly conspicuous cytoplasmic strands connecting the cells one to another. Other genera have no visible strands, but the behavior of severed fragments of colonies furnishes indirect evidence that the cells are in cytoplasmic connection.[1]

All colonies are *coenobia*, that is, colonies with a definite number of cells arranged in a specific manner. Coenobia of most genera exhibit a definite polarity when swimming through the water, one pole of the globose or ellipsoidal colony always being directed forward. There may also be an evident morphological anterior-posterior differentiation, either in size of eyespots of cells at opposite poles of the coenobium or in outline of the colonial envelope. In certain advanced genera all cells toward the anterior pole are vegetative and reproductive cells lie toward the posterior pole.

Daughter coenobia are always formed by repeated division of a single cell and according to a definite sequence (Fig. 12). All divisions are longitudinal, and all cells of each cell generation divide simultaneously. The four cells of the second cell generation are quadrately disposed; the eight of the third generation are cruciately disposed and with a tendency to form a curved plate or *plakea*. In all but one genus, the plakea becomes a hollow sphere with a small opening, the *phialopore*, at what will eventually become the posterior pole of the colony. Some genera, as *Pandorina*, stop dividing at or before the 32-celled stage; other genera, as *Eudorina*, do not develop beyond the 64-celled stage. In one genus (*Volvox*) division continues until there are thousands of cells. Until fairly late in development of a daughter coenobium, the nucleus in each cell lies toward the inner face of the colony; later stages have the nuclei toward the outer face of each cell. This change in position is due to the colony turning itself inside out (inverting) through the phialopore during later stages of development.

The three genera described below illustrate the three major evolutionary tendencies among the Volvocaceae. These are: (1) an increase in number of cells in the colony; (2) an advance from a condition where all cells are reproductive to one where only certain of them are reproductive; and (3) an advance from isogamy to anisogamy to oögamy.

[1] Bock, 1926.

Pandorina, with three species, is widespread but rarely found in abundance. The colonies are subspherical to ellipsoidal and have 4, 8, 16, or 32 biflagellate cells embedded within a homogeneous gelatinous matrix (Fig 9*A*). There may also be an outer colonial sheath of a more watery consistency. The cells are arranged in a hollow sphere within the colonial envelope and are generally so close together that they are laterally flattened by mutual compression, but in one species[1] they are not in lateral contact with one another Laterally abutting cells are pyriform and have the two flagella and the eyespot borne on the broad anterior end There are always two contractile vacuoles

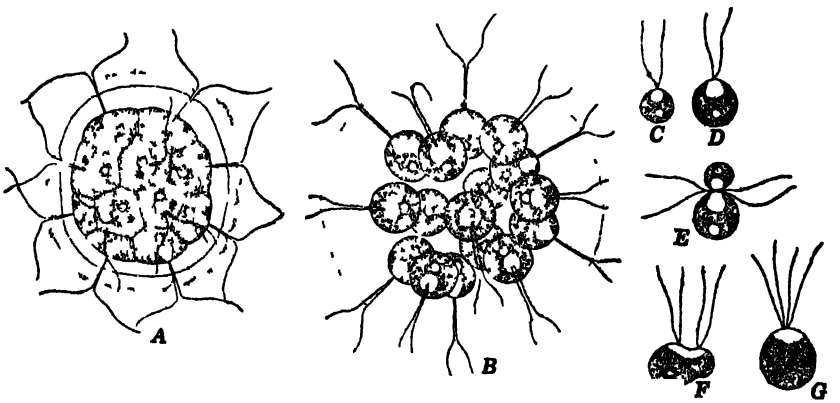


FIG 9 *Pandorina morum* Bory *A* vegetative colony *B*, colony of female gametes *C*, male gamete *D* female gamete *E F* gametic union *G*, motile zygote (× 650)

at the base of the flagella The chloroplast is massive and cup-shaped; it may have a smooth outer face and contain a single pyrenoid, or its outer face may be longitudinally ridged and it may contain several pyrenoids.

At the time of asexual reproduction there is usually a simultaneous division of each cell of the coenobium into a daughter coenobium. Just before reproduction a colony ceases active movement, it sinks to the bottom of the pool, and the colonial envelope becomes more watery and swells. The first three longitudinal divisions of a cell produce a typical eight-celled plakea with four of the cells cruciately arranged.[2] Simultaneous longitudinal division usually continues until there are 16 or 32 cells. Inversion of a developing coenobium has not been recorded for *Pandorina*, but there is a strong presumption that a young coenobium inverts. The newly formed daughter colonies escape by swimming directly through the gelatinized envelope of the parent colony.

Divisions leading to the formation of biflagellate gametes are identical with those in asexual reproduction However, the group of daughter

[1] Smith, G M , 1931 [2] Chodat, 1894; Dangeard, 1900

cells destined to function as gametes are arranged in a *Eudorina*-like manner and are surrounded by a broad watery sheath (Fig. 9*B*). The group of cells swim about through the water as a colony-like unit, but sooner or later the individual cells (the gametes) escape from the common gelatinous matrix and swim about singly.[1] The fusing biflagellate gametes are always unequal in size and the larger, the female, may be more sluggish than the male (Fig. 9*C–G*). Fusion may be lateral or terminal. The quadriflagellate zygote remains motile for a very short time; then it loses its flagella and secretes a wall. Old zygotes have a smooth thick wall and a protoplast colored red by haematochrome.

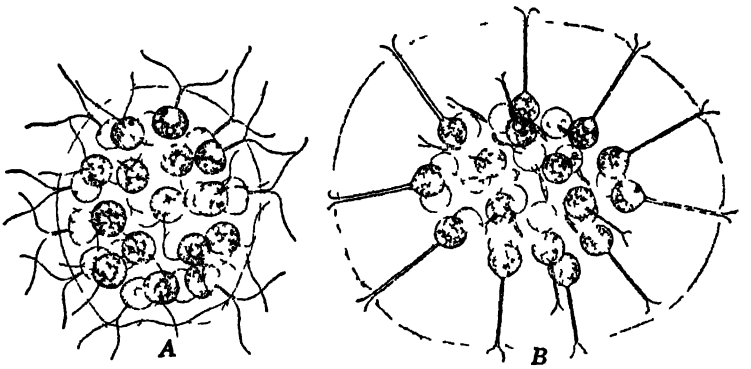


FIG. 10.—*A*, *Eudorina unicocca* G. M. Smith. *B*, female colony of *E. elegans* Ehr. in which there are male gametes swimming within the colonial envelop. (*A*, × 435, *B*, × 235.)

When a zygote germinates,[2] the contents are extruded in a vesicle, and the irregularly green and orange protoplast soon develops two flagella and swims away as a single zoospore. Sometimes a germinating zygote produces two or three zoospores. After swarming for a time, a zoospore retracts its flagella, secretes a broad gelatinous envelope, and divides and redivides to form a typical colony.

Eudorina, with four or five species, is widespread in fresh water and is sometimes present in abundance in small puddles. Its colonies are spherical or obovoid and have a homogeneous colonial envelope that may have mamillate projections at the posterior pole.[3] The 16, 32, or 64 cells in a colony lie some distance from one another and toward the periphery of the colonial envelope. Frequently the cells are in distinct transverse tiers (Fig. 10*A*). If the colonies are 32-celled, the anterior and posterior tiers contain four cells each and the three median tiers eight cells each.[4] The individual cells are spherical, and all are of approximately the same

[1] Pringsheim, 1870; Smith, G. M., 1933; Meyer, K. I., 1935.
[2] Pringsheim, 1870. [3] Smith, G. M., 1931.
[4] Chodat, 1902; Conrad, 1913; Hartmann, 1921; Smith, G. M., 1931.

size. The length of the flagella is two to four times the diameter of a mature cell, and the cells may be with or without a conical elevation where the flagella are inserted. There are two contractile vacuoles at the base of the flagella. The single eyespot lies at the anterior end of a cell. Certain species have a progressive diminution in size of eyespots from anterior to posterior cells of a colony, and eyespots may even be lacking in the lowermost tier of cells. The chloroplast is cup-shaped and massive and, according to the species,[1] contains one or several pyrenoids. The cells are connected to one another by very delicate cytoplasmic strands.[2]

At the time of asexual reproduction all cells of a colony usually divide to form daughter colonies, but occasionally one or more cells fail to divide. The sequence of division is in the manner typical of Volvocaceae, and *Eudorina* has been shown[3] to have an inversion of the plakea. The newly formed daughter colonies escape by swimming directly through the gelatinized envelope of the parent colony.

A vegetative colony may become an amorphous palmelloid mass. Development of such *Palmella* stages is due to gradual desiccation, and within a few minutes after reflooding the palmelloid cells develop flagella and escape as solitary zooids.[4] A free-swimming zooid may develop into a typical colony the night after liberation. Instead of developing into a *Palmella* stage, a colony may have its cells losing their flagella and developing into akinetes.[5]

The anisogamous sexual reproduction of *Eudorina* shows a very close approach to oogamy in that the female gametes are not free-swimming and in that the gametes are dissimilar in size and shape. Certain species are heterothallic.[6] Other species are homothallic[7] and usually have the four anterior cells dividing to form male gametes and the remaining cells functioning as female gametes. Divisions forming the male gametes are according to the same sequence as in asexual reproduction and usually continue until there are 64 spindle-shaped biflagellate male gametes arranged in a flat or curved plakea. Heterothallic species have the packets of male gametes escaping from the old colonial matrix, swimming about as a unit through the water, and dissociating into individual gametes when the packet comes near a female colony. Vegetative cells of female colonies function directly as female gametes, and there is no evident change other than a swelling of the gelatinous colonial matrix.

The male gametes swim directly into the colonial matrix of a female colony and there fuse with the female gametes (Fig. 10*B*). The zygotes remain within the female colony until liberated by decay of the colonial

[1] Smith, G. M., 1931. [2] Bock, 1926; Conrad, 1913. [3] Hartmann, 1924.
[4] Schreiber, 1925. [5] Pascher, 1927.
[6] Goebel, 1882; Goroschankin, 1875; Schreiber, 1925; Smith, G. M., 1931.
[7] Carter, H. J., 1858; Iyengar, 1933; Meyer, K. I., 1935.

envelope. A mature zygote has a smooth wall and a protoplast deeply colored with haematochrome. The first step in its germination is a swelling of the wall and a formation of a sac-like extension at one side.[1] Usually the vesicle contains one reddish zoospore and two or three small hyaline bodies which are probably degenerate zoospores. A zoospore swims about for a time after liberation from the vesicle and then, in the same manner as a vegetative cell, divides and redivides to form a colony.

Volvox, with a dozen or more species, is found in both temporary and permanent fresh-water pools. Sometimes it is present in sufficient

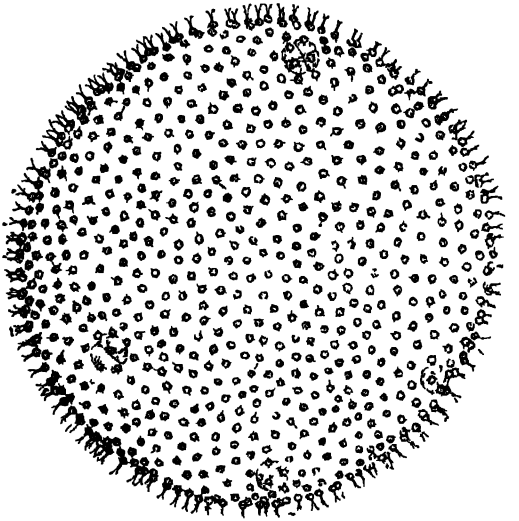


FIG. 11.—Vegetative colony of *Volvox aureus* Ehr (× 200.)

abundance to color the water green. It usually appears in the spring, increases in abundance, and then disappears abruptly[2] early in the summer. During the remainder of the year, it is in a resting zygote stage

The colonies are spherical to ovoid and with 500 to 40,000 cells that lie in a single layer within the periphery of the colonial matrix (Fig. 11). Each cell is surrounded by a gelatinous sheath of its own, and sheaths of cells may be confluent or distinct from one another. In the latter case they are angular by mutual compression and usually hexagonal. The central portion of a colony may contain gelatinous material of a more watery consistency, or it may contain water only.[3] Some species have ovoid to ellipsoidal cells; others have pyramidal cells with the broad base facing the interior of the colony. A majority of species have the cells joined to one another by conspicuous or delicate cytoplasmic strands, and

[1] Otrokov, 1875; Schreiber, 1925. [2] Pocock, 1933; Smith, G. M., 1917.
[3] Janet, 1912, 1922; Lander, 1929; Meyer, A., 1895.

these connections are established during the course of cell divisions producing the colony.[1]

Most of the cells of a colony are vegetative in function and are incapable of giving rise to new colonies or to gametes. A vegetative cell has two flagella at its anterior end and either two contractile vacuoles near the base of the two flagella or two to five contractile vacuoles irregularly distributed throughout the anterior end. There is a cup-shaped or laminate chloroplast and usually only one pyrenoid within a chloroplast. The nucleus is centrally located and is connected with the flagella by a neuromotor apparatus of the blepharoplast-rhizoplast-centriole type.[2] Each vegetative cell has a single eyespot toward its outer face, and those of cells toward the anterior pole of a colony are somewhat larger than those of cells toward the posterior pole.

Young colonies have all cells alike in size. As a colony grows older, certain cells in the posterior half increase to ten or more times the diameter of vegetative cells and develop numerous pyrenoids within their chloroplasts. These enlarged cells are reproductive cells, and their reproduction may be sexual or asexual. All reproductive cells of a colony are asexual in nature or all are sexual. Reproduction is exclusively asexual at the beginning of the growing season and exclusively sexual at the end of the season.

Colonies reproducing asexually have 5 to 20 reproductive cells, and each of them produces a daughter coenobium. Development begins with a longitudinal division, and all succeeding divisions are longitudinal and simultaneous (Fig. 12). The 8-celled stage is the usual cruciate plakea, and the 16-celled stage is a hollow sphere with a phialopore at the outer pole. Simultaneous division continues for several cell generations.[3] In the largest known species (*V. Rousseletii* G. S. West) there are 14-, 15-, or 16-cell generations beyond the two-celled stage.[4] Theoretically this would produce colonies with 16,384 (2^{14}), 32,768 (2^{15}), or 65,536 (2^{16}) cells, but this number is not attained because some cells of the last few cell generations fail to divide. When cell division ceases, the young colony turns itself inside out (Fig. 12*G*) by invaginating (inverting) through the phialopore.[5] This process may be compared to turning a glove inside out. Inversion is accomplished in from three to five hours.[4] Flagella are developed shortly after inversion, and the daughter colony then revolves slowly within the greatly enlarged old parent-cell wall. Some species have an escape of daughter colonies through a pore in the outer face of the parent-cell wall.[4] Other species seem to fail to develop such a pore but retain their daughter colonies within the parent colony

[1] Janet, 1912; Meyer, A., 1896; Pocock, 1933*A*.
[2] Zimmermann, 1921.
[3] Janet, 1923.
[4] Pocock, 1933*A*.
[5] Kuschakewitsch, 1931; Lander, 1929; Pocock, 1933, 1933*A*; Powers, 1908.

until the latter dissociates or ruptures. Such species may have the imprisoned daughter colonies also forming daughter colonies before they are liberated.

Sexual reproduction is oogamous and may be homothallic or heterothallic. Reproductive cells destined to develop into sex organs lie in the posterior half of a colony, and their number varies from a dozen to several

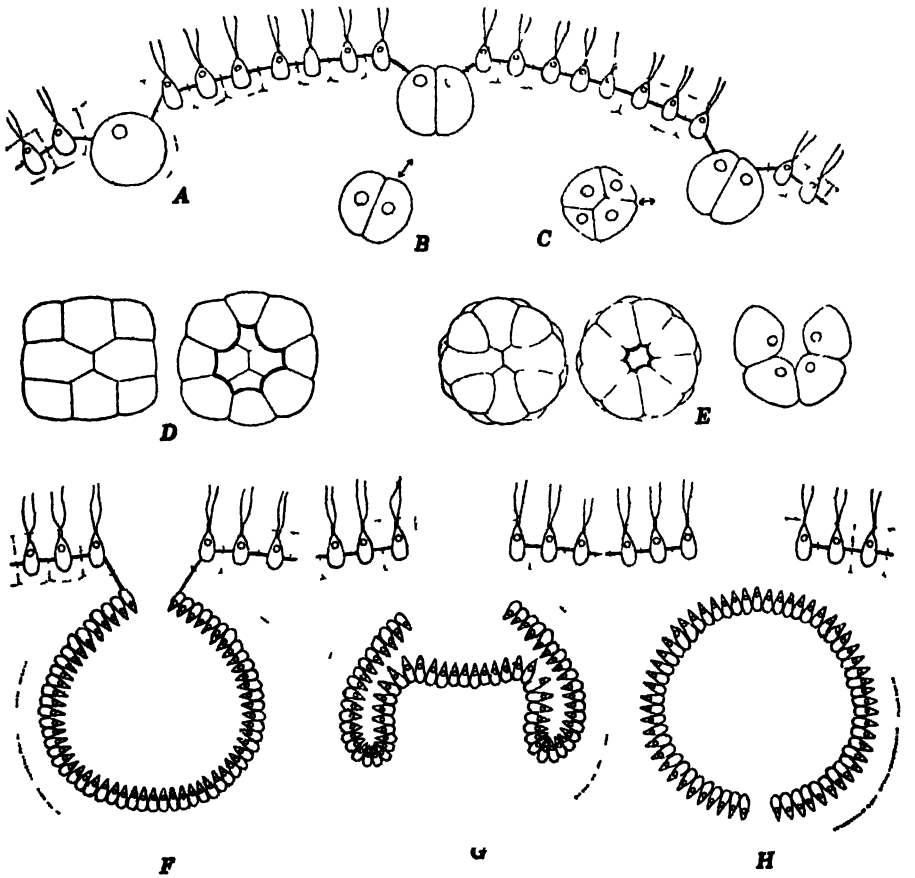


FIG 12.—Diagrams showing stages in development of a daughter colony of *Volvox* *A–E*, one-, two- four-, eight-, and sixteen-celled stages *F*, just before inversion. *G*, inversion *H*, after inversion.

hundred. The male sex organs (the *antheridia*) differ from antheridia of other oogamous Chlorophyceae in that the male gametes (*antherozoids*) may be liberated in a definitely organized colony-like mass instead of individually Division of the protoplast of an antheridium is by a successive bipartition and according to the same sequence as in asexual reproduction (Fig 13*A*) Some species have division stopping at the 64- or the 128-celled stage. In these species the entire mass of fusiform

biflagellate antherozoids is liberated as a plate-like colony that swims about as a unit until it approaches the vicinity of an egg Other species[1] have bipartition of the antheridial protoplast continuing beyond the 128-celled stage, and the antherozoids are arranged in a hollow sphere that inverts in the same manner as an asexual colony Antherozoids of these species are liberated singly and gradually from an antheridium.

Oogonia resemble asexual reproductive cells; and in each of them the protoplast metamorphoses into a single spherical nonflagellated egg (Fig.

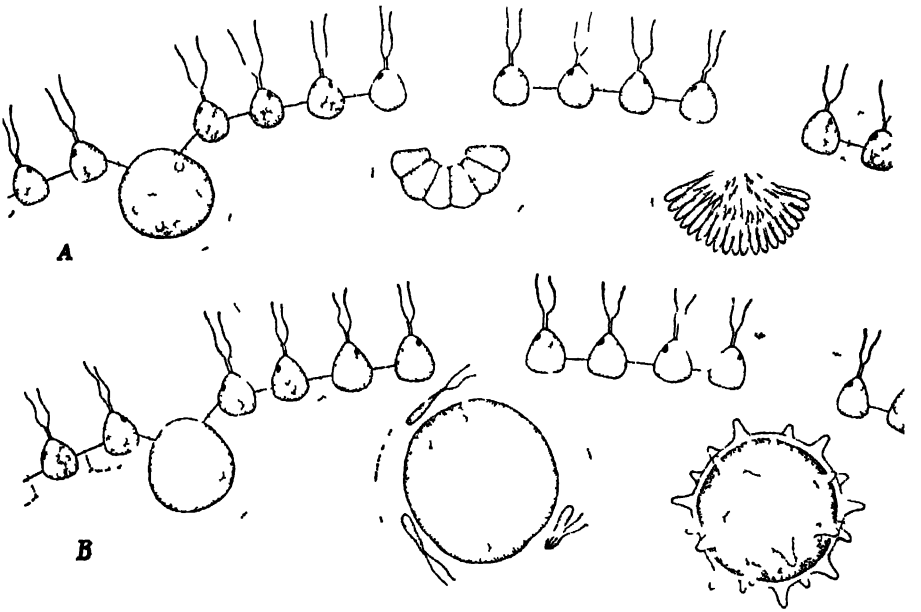


FIG 13.—*Volvox* sp *A* portion of a male colony showing development of antheridia *B*, portion of a female colony showing a young egg fertilization and a ripe zygote (Both figures diagrammatic) (× 1 300)

13*B*). When fertilization takes place, the individual antherozoids swim through the oogonial wall and move slowly about within the oogonium Unfertilized eggs may develop into parthenospores with a structure similar to that of zygotes[2]

The zygote secretes a smooth or stellate, three-layered wall and develops sufficient haematochrome to color the protoplast an orange-red: The zygotes are retained in the parent colony until the latter decays or disintegrates. Then they fall to the bottom of the pool, where they may ripen for several months before germinating They remain viable for several years and germination may be long delayed if conditions are unfavorable[3] Germination is preceded by a reduction division of the zygote nucleus.[3] At the time of germination there is a splitting of the

[1] Pocock, 1933, 1933*A* [2] Mainx, 1929 [3] Pocock, 1933*A*

outer zygote wall layer (the *exospore*) and an expulsion of the protoplast still surrounded by the two inner wall layers.[1] The median wall layer (*mesospore*) then splits, and the delicate inner wall layer (*endospore*) protrudes to form a vesicle into which the protoplast migrates. In *V. aureus* Ehr. there is[2] a direct development of the protoplast into a colony by the same sequence of plakeal stages as in asexual reproduction. In *V. capensis* Rich and Pocock the protoplast develops into a large biflagellate zoospore that escapes from the vesicle.[1] The free-swimming zoospore begins to form a colony while it is still actively motile, and the flagella do not disappear until several successive divisions have taken place.

ORDER 2. TETRASPORALES

The Tetrasporales have immobile vegetative cells which may temporarily metamorphose into a flagellated motile stage. Most genera have the cells united in nonfilamentous colonies that are either amorphous or of a definite shape. A few genera have solitary cells. Asexual reproduction is by means of zoospores, aplanospores, or akinetes. Sexual reproduction is isogamous and by the fusion of biflagellate gametes.

The order includes approximately 35 genera and 100 species, almost all of them fresh-water in habit.

Typical Tetrasporales may be looked upon as unicellular Volvocales in which the cells are usually in an immobile palmelloid condition and only temporarily revert to a motile condition. The more or less permanently palmelloid vegetative cells of certain genera[3] have such chlamydomonad characters as eyespots, contractile vacuoles, and flagella or flagella-like structures.

Many phycologists hold that these genera are too closely related to the chlamydomonad type to warrant segregation from the Volvocales. They assign them and all other tetrasporaceous algae to the Volvocales and do not recognize the Tetrasporales as a distinct order. However, those who favor this practice admit that the immobility of these primitively organized cells is a step in advance of the temporary immobility found in *Palmella* stages of Chlamydomonadaceae. The tetrasporaceous Chlorophyceae are divided into three[4] or into four[5] families.

Tetraspora is a fresh-water genus with about 20 species. Its cells are spherical to ellipsoidal and united in many-celled colonies by a homogeneous gelatinous matrix. There is a certain tendency for the cells to lie in groups of two or four within the matrix, but in many colonies they are irregularly scattered. Fully developed colonies of *Tetraspora* are

[1] Pocock, 1933*A*. [2] Kirchner, 1883.
[3] Korshikov, 1926; Lambert, 1930; Pascher, 1927.
[4] Fritsch, 1935. [5] Smith, G. M., 1933.

usually several centimeters in diameter (Fig. 14*A–B*). The colonial matrix of most species is of so watery a consistency that the colony breaks in pieces when one attempts to lift it from the water, but in certain species, as *T. cylindrica* (Wahlb) C A Ag , the matrix is tough and firm

The cells[1] lie toward the periphery of the colonial envelope, and the face toward the exterior of the colony bears two long, immobile, flexible cytoplasmic processes (*pseudocilia*), which may extend only to the

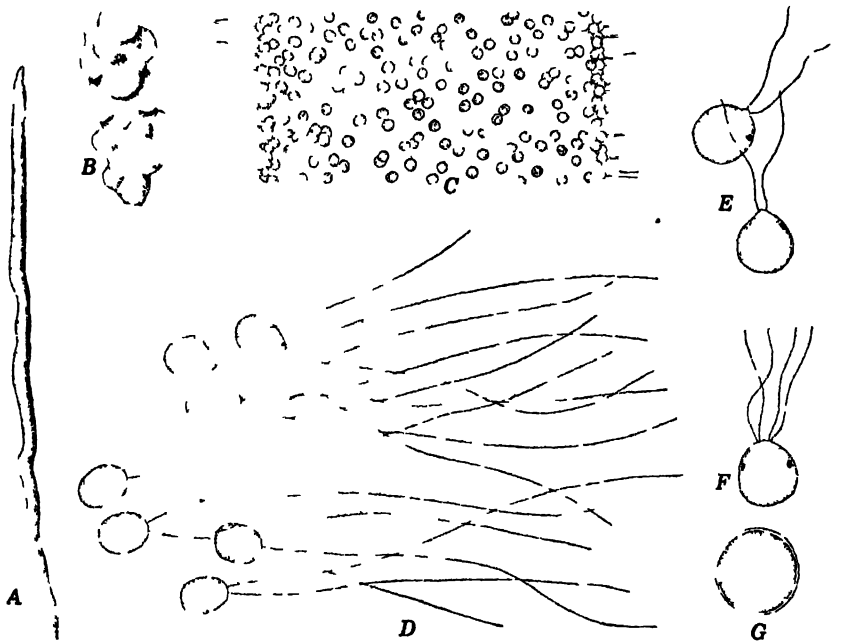


FIG 14 —*A* colony of *Tetraspora cylindrica* (Wahlb) C A Ag *B* colony of *T lubrica* (Roth) Ag *C* portion of colony of *T cylindrica* *D G T gelatinosa* (Vauch) Desv *D*, vegetative cells with pseudocilia *E* gametes *F* motile zygote *G*, old zygote (*A B*, × ½ *C*, × 155, *D*, × 1300 *E G* × 650)

surface of the colonial envelope or may extend beyond it (Fig 14*C*) All species have pseudocilia, but they are not always evident in all colonies of a species Within the cell are a nucleus and a massive cup-shaped chloroplast containing a single pyrenoid Cells of old colonies often have the chloroplasts so densely packed with starch that the structure of the chloroplast is obscured.

Growth of a colony is by the cells dividing into two or four daughter cells. Cytokinesis in cells of *Tetraspora* is by means of a cell plate developed on the mitotic spindle.[2] The old parent-cell wall gelatinizes to form a special envelope about the group of daughter cells (Fig. 14*D*). The envelope is quite distinct immediately after cell division, but it

[1] Klyver, 1929; Schröder, 1902 [2] McAllister, 1913

gradually merges with the colonial matrix as the daughter cells increase in size and become more remote from one another. Colonies may grow to over a meter in length, but they usually become broken in smaller pieces before they attain such a size. At any time in the development of a colony, all or certain of the cells may be metamorphosed into biflagellate zoospores. The zoospores escape from the colonial matrix and swim about for a short time: then they withdraw their flagella, secrete a gelatinous envelope, and develop into new colonies by vegetative cell division. Vegetative cells may also develop into thick-walled akinetes (hypnospores) with brown sculptured walls. Germinating hypnospores have[1] an amoeboid liberation of the protoplast, and it may remain amoeboid through several cell generations before assuming the usual shape and structure of a vegetative cell.

Sexual reproduction is by the fusion of biflagellate gametes. Certain species are heterothallic.[2] The protoplast of a cell divides to form four or eight zoogametes that escape from the colonial matrix. Gametes differ from zoospores in that they have a more pronounced pyriform shape, a more distinctly cup-shaped chloroplast, and an eyespot at the anterior end (Fig. 14*E–G*). They become apposed in pairs at their anterior ends and fuse laterally.[3] The zygote swarms for a short time after its formation but eventually comes to rest, secretes a wall, and grows to twice its original diameter. When it germinates, the protoplast divides to form four or eight aplanospores which lie within a common matrix formed by gelatinization of the old zygote wall. The vegetative cells formed by germination of these aplanospores remain within the common matrix and so constitute a compound colony.[3]

ORDER 3. ULOTRICHALES

The Ulotrichales have uninucleate cells (with the exception of old cells of certain genera) and usually a single parietal laminate chloroplast. The cells are united end to end in simple or branched filaments. Certain branching filamentous genera have their branches apposed in a pseudoparenchymatous mass or are reduced to an irregularly shaped few-celled structure. In one genus (*Protococcus*) the filament is reduced to a single cell. The usual method of asexual reproduction is a formation of bi- or quadriflagellate zoospores, but aplanospores and akinetes are not at all uncommon. Gametic union is found in many genera of the order and may be isogamous, anisogamous, or oögamous.

There are about 80 genera and 430 species. Most of the genera are exclusively fresh-water, but a few have some marine species and a few others are exclusively marine.

[1] Pascher, 1915. [2] Geitler, 1931. [3] Klyver, 1929.

The branching characteristic of a majority of the genera represents a more advanced condition than does the simple filament. Ulotrichales with a branching thallus often have it differentiated into a prostrate and an erect portion. Because of this the branching genera have been thought[1] to have an organization fundamentally different from unbranched filamentous genera and have been placed in a distinct order.

The Ulotrichales appear to have been evolved directly from the Tetrasporales. Evolution of a tetrasporaceous type of plant body into a ulotrichaceous filamentous type might have been due to a limiting of cell division to one plane only and an accompanying failure to develop gelatinous material between the daughter cells. Certain Tetrasporales have a tendency toward a filamentous organization in that most of the cell divisions are in the same plane.[2] Some of the Ulotrichales appear to be so closely related to the Tetrasporales that they have not lost the capacity for secreting gelatinous material between the daughter cells. However, it is much more probable that these Ulotrichales are ones that have reverted to a permanently filamentous *Palmella* stage. The frequent occurrence of *Palmella* stages among primitive families of the order (Ulotrichaceae, Chaetophoraceae) as contrasted with their rare occurrence among advanced families (Coleochaetaceae, Trentepohliaceae) is good evidence that the Ulotrichales have been derived from ancestors with a palmelloid organization.

It is very probable that the Ulotrichales are haplontic and with a multicellular haploid generation alternating with a one-celled diploid phase. This has been demonstrated for two genera (*Ulothrix*, *Coleochaete*), and it seems also to be true of several other genera known to have a production of four zoospores by the germinating zygote.

The seven families of the order are primarily distinguishable from one another on the basis of vegetative structure (especially organization of the filament), wall structure, and chloroplast structure.

FAMILY 1. ULOTRICHACEAE

The Ulotrichaceae include all the unbranched filamentous genera in which the cells are uninucleate and have a single parietal girdle-shaped chloroplast. The cell walls are homogeneous and are not composed of overlapping pieces. Almost all genera are known to produce bi- or quadriflagellate zoospores. Asexual reproduction by means of aplanospores or akinetes is also not infrequent. Sexual reproduction is known for but few genera, and all cases thus far recorded are isogamous and have a fusion of motile gametes.

There are about 15 genera and 110 species, almost all of them freshwater.

[1] Fritsch, 1916, 1935; West and Fritsch, 1927. [2] Smith, G. M., 1933.

Ulothrix, with about 30 species, has a large majority of its species growing in fresh water. Some species, especially *U. zonata* (Weber and Mohr) Kutz., are distinctly cold-water plants; appearing in early spring, disappearing during the summer, and then reappearing in the fall. The cells of *Ulothrix* are united end to end in unbranched filaments of indefinite length (Fig. 15*A*). All cells but the rhizoidal basal one may divide vegetatively or may produce zooids. The cell walls may be thick or thin and homogeneous or stratified. A few species have broad gelatinous sheaths about the filaments, but in most species a sheath is not evident. The cells are always uninucleate and with a single girdle-shaped chloro-

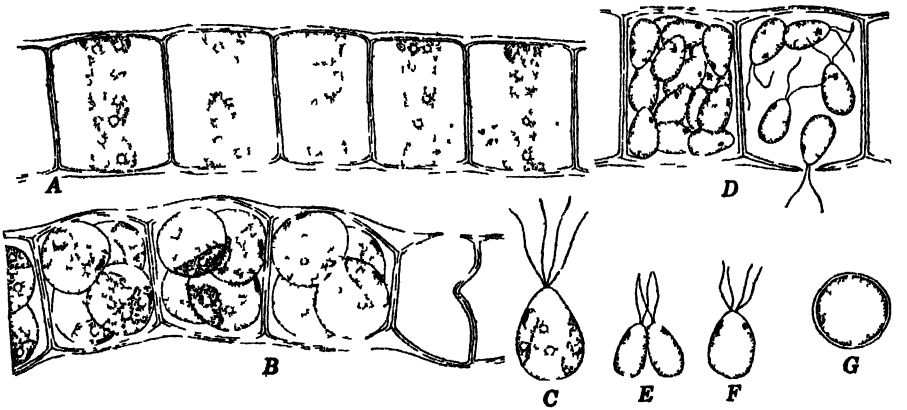


FIG. 15.—*Ulothrix zonata* (Weber and Mohr) Kutz *A*, vegetative cells *B*, formation of zoospores *C*, zoospore *D*, gametes. *E F*, gametic union *G*, zygote. (× 1000)

plast that partially or completely encircles the protoplast. According to the species, the chloroplast extends the whole length of a cell or only a part of its length, and contains one or several pyrenoids.

Vegetative multiplication may be due to an accidental breaking of a filament or, in very rare cases,[1] to its dissociation into many fragments with a few cells each.

All cells but the holdfast may produce zoospores, but those in the distal portion of a filament usually produce them in advance of those in the lower portion. Species with narrow cells produce 1, 2, or 4 zoospores per cell; those with broad cells produce 2, 4, 8, 16, or 32 zoospores in each cell (Fig. 15*B*). The protoplast of a cell about to produce zoospores contracts slightly and becomes filled with reserve food material. If more than one zoospore is to be produced, the nucleus divides and the protoplast cleaves in a plane at right angles to the long axis of the filament. The nucleus in each daughter protoplast may also divide and both protoplasts cleave in a plane perpendicular to that of the first cleavage.[2] Simultaneous bipartition may continue until there are 32 daughter

[1] Gross, 1931; Lind, 1932 [2] Cholnoky, 1932; Gross, 1931; Lind, 1932.

protoplasts. When cleavage ceases, each of the daughter protoplasts is metamorphosed into a quadriflagellate zoospore with a conspicuous eyespot (Fig. 15*C*). The zoospores are liberated through a pore in the side of the parent-cell wall. The spore mass is usually surrounded by a thin vesicle when first extruded, but this disappears within a minute or two. All zoospores from a filament of a narrow-celled species are alike in size. Filaments of broad-celled species, as *U. zonata*, produce quadriflagellate macro- and microzoospores that differ from each other in size, position of eyespot, and length of swarming period.[1] Zoospores which are not discharged from a parent cell may each secrete a wall and become thin-walled aplanospores. Many of these aplanospores germinate before they are liberated from the parent-cell wall.[2] The protoplast of a vegetative cell may also round up to form a single large thick-walled aplanospore.[3]

Gametes (Fig. 16*D–F*) are formed in the same manner as zoospores, but the number formed is 8, 16, 32, or 64.[4] They are biflagellate, all of the same size, pyriform, and with an eyespot. They fuse in pairs with one another, but fusion only takes place between gametes coming from different filaments.[5] There is no parthenogenetic development of gametes into vegetative filaments.[6] The zygote (Fig. 16*G*) remains motile for a short time and then comes to rest, secretes a thick lamellated wall, and enters upon a resting period during which there is a considerable accumulation of reserve food. The first division of a zygote nucleus is reductional.[6] The protoplast of a germinating zygote divides into 4 to 14 (16?) daughter protoplasts which develop into aplanospores[7] or into zoospores.[2]

FAMILY 2. MICROSPORACEAE

The Microsporaceae have an unbranched filament in which the cells contain a single variously lobed chloroplast. The wall of a cell consists of two pieces that are H-shaped in optical section.

The single genus *Microspora* has about 14 species. They are all fresh-water, grow in pools and ditches, and are most abundant during early spring.

The walls of a filament are a linear file of segments that are H-shaped in optical section. The segments are so articulate that each protoplast is enclosed by the conjoined halves of two successive H-pieces (Fig. 16*A*). The H-pieces are heavily impregnated with cellulose[8] and sometimes are distinctly stratified. Internal to the H-pieces is a very thin layer of

[1] Klebs, 1896; Pascher, 1907. [2] Dodel, 1876. [3] West, G. S., 1916.
[4] Dodel, 1876; Gross, 1931; Klebs, 1896; Lind, 1932; Pascher, 1907; West, G. S., 1916.
[5] Cholnoky, 1932; Gross, 1931; Lind, 1932 [6] Gross, 1931.
[7] Jørstad, 1919; Klebs, 1896. [8] Tiffany, 1924.

cellulose completely encircling the protoplast.[1] At the time of cell division there is a development of a thin layer of cellulose about each daughter protoplast and an intercalation of a short H-shaped piece of wall material between the two. This new H-piece gradually lengthens as the two H-pieces that formerly enclosed the parent cell pull apart from each other.

The cells are uninucleate and generally with the nucleus lying in a bridge of cytoplasm across the middle of the central vacuole. There

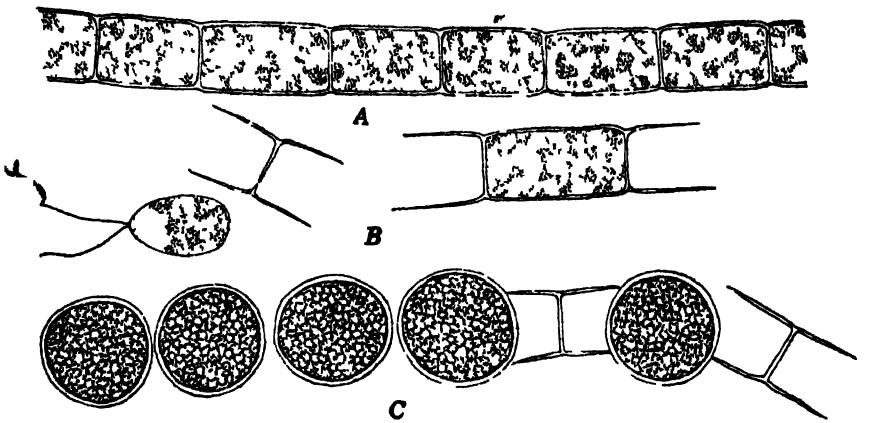


FIG. 16.—*Microspora Wuleana* Wittr. *A*, vegetative cells. *B*, liberation of zoospore. *C*, aplanospores (× 900)

is usually so much reserve starch in a cell that but little can be made out concerning structure of the chloroplast. In young, vigorously growing cells, the chloroplast is an irregularly expanded, perforate or reticulate sheet covering both the sides and ends of the protoplast. Pyrenoids are lacking in chloroplasts of *Microspora*.[2]

Asexual reproduction is by the formation of 1, 2, 4, 8, or 16 zoospores within a cell. When more than one zoospore is formed, there is a bipartition of the protoplast after each mitosis.[3] The zoospores may be liberated by a disarticulation of the H-pieces of the wall of the parent cell (Fig. 16*B*), or there may be a gelatinization of the sides of the H-pieces and a swimming of zoospores through the gelatinized portions. The zoospores are biflagellate, are naked, and have a hyaline anterior end.[4] Quadriflagellate zoospores have been recorded[5] for one species. A zoospore swarms for a short time and then comes to rest and secretes a wall. The germling thus formed may be free floating, or it may be sessile and affixed by a discoid holdfast. Aplanospores may also be formed. They are usually spherical and are formed singly within a cell (Fig. 16*C*).

[1] Tiffany, 1924 [2] Lagerheim, 1889; West, G. S., 1916. [3] Meyer, K., 1913.
[4] Hazen, 1902; West, G. S., 1916.

Germinating aplanospores develop directly into new filaments.[1] Some species also form thick-walled akinetes in abundance. They may contain 2, 4, 8, or 16 nuclei.[1] If they germinate within a few days, there is a direct development into a new filament. If germination is long delayed, the contents divide into four daughter protoplasts, either before or after escape from the old wall, and each daughter protoplast develops into a new filament.[2]

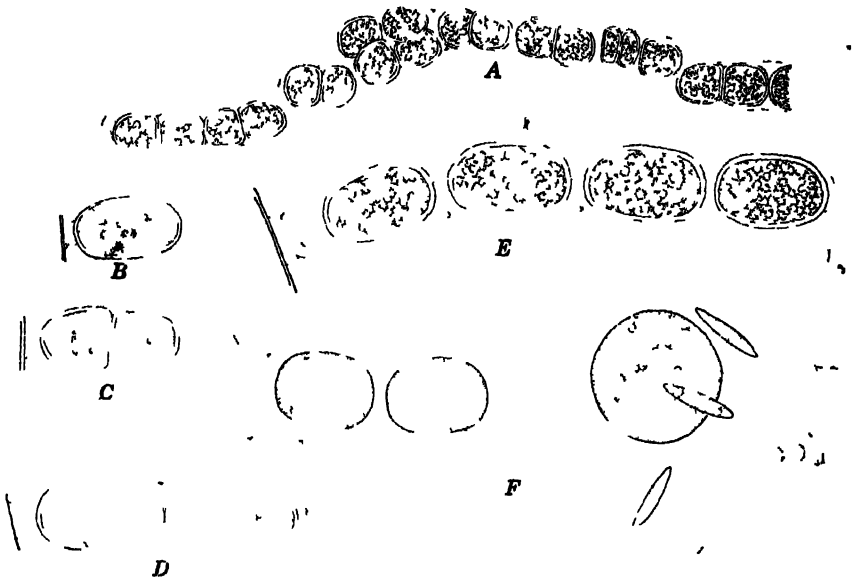


FIG. 17.—*A*, *E*, *Cylindrocapsa geminella* Wolle. *A*, old filament. *B*, *E*, germination stages. *F*, *C. involuta* Reinsch (*after* Cienkowski, 1876) oogonium at time of fertilization (*A*, × 325, *B*, *E*, × 650, *F*, × 180.)

The single recorded case of gametic union[3] is open to question since there is a possibility that the alga studied was *Tribonema* rather than *Microspora*.

FAMILY 3. CYLINDROCAPSACEAE

The Cylindrocapsaceae have unbranched filaments in which the cells have concentrically stratified walls. They differ from other unbranched Ulotrichales in that their sexual reproduction is oogamous.

The single genus, *Cylindrocapsa* (Fig. 17*A*), is fresh-water and has five species. Under certain conditions of growth there is a complete loss of the filamentous organization and a development of *Palmella* stages in which the cells are irregularly arranged. Each protoplast in a filament is enclosed by a cellulose wall[4] which is laid down in concentric strata.

[1] Meyer, K., 1913. [2] West, G. S., 1916. [3] Steinecke, 1932.
[4] Tiffany, 1924.

The whole filament is surrounded by a tough gelatinous sheath of a pectic nature. Old cells are so densely packed with starch that the structure of the chloroplast is obscured. Young cells contain a massive chloroplast with a single pyrenoid.

There may be a vegetative multiplication by a fragmentation of filaments. Asexual reproduction is by means of biflagellate zoospores with two contractile vacuoles and an eyespot.[1] Germination stages of zoospores are sessile and affixed to the substratum by a gelatinous holdfast. Cell division in young filaments (Fig. 17*B*-*E*) is transverse, and each daughter cell develops a wall with several concentric strata.

Sexual reproduction is oögamous,[1] and both gametes are developed in the same filament. Cells developing into sex organs may be distinguished from vegetative cells by their reddish color. In the formation of antheridia certain vegetative cells divide and redivide to form a double file of small red-colored spherical antheridia, each of which produces two antherozoids. The antherozoids are fusiform and have two short flagella. The protoplast of a cell developing into an oogonium increases in volume, and the surrounding cell wall becomes greatly swollen. Just before fertilization there is a formation of a pore at one side of the swollen oögonial wall. Fertilization (Fig. 17*F*) takes place by an antherozoid swimming into an oögonium through the pore in the wall and fusing with the egg within the oogonium. Ripe zygotes are spherical and have a smooth thick wall enclosing a bright-red protoplast.

FAMILY 4. CHAETOPHORACEAE

The Chaetophoraceae have a branching filamentous thallus in which the branches may be free from one another or pressed together into a pseudoparenchymatous tissue. The terminal cell or cells of a branch may be prolonged into a long colorless seta. The cells are uninucleate and usually have a single laminate parietal chloroplast. Asexual reproduction may be by means of zoospores, aplanospores, or akinetes. Sexual reproduction is usually isogamous, but it may be anisogamous or oögamous.

There are about 50 genera and 225 species. Most of the Chaetophoraceae are fresh-water algae.

Typical members of the family have *Ulothrix*-like cells united in branching filaments. Most genera have the plant body differentiated into a prostrate portion and an erect, freely branched portion. The erect portion may have all branches the same size, or there may be a differentiation into large primary and small lateral branches. There are no life-cycle studies showing whether the Chaetophoraceae have or lack an alternation of generations. The presumption is that they are haplontic.

[1] Cienkowski, 1876.

Stigeoclonium, with some 35 species, is a common fresh-water algae. It grows in standing or flowing water and affixed to stones, woodwork, and submerged aquatics. The plant body is differentiated into a prostrate and an erect portion. The prostrate portion, which attaches the alga to the substratum, is either pseudoparenchymatous or irregularly branched. It bears many erect branches. They are sparsely branched, with an alternate or opposite branching, and have the obscure main axis and the lateral branches attenuated into long multicellular hairs (Fig. 18*A*). Erect branches are often enclosed by a broad gelatinous sheath, but this is of a very watery consistency and not usually visible unless demonstrated by special methods.

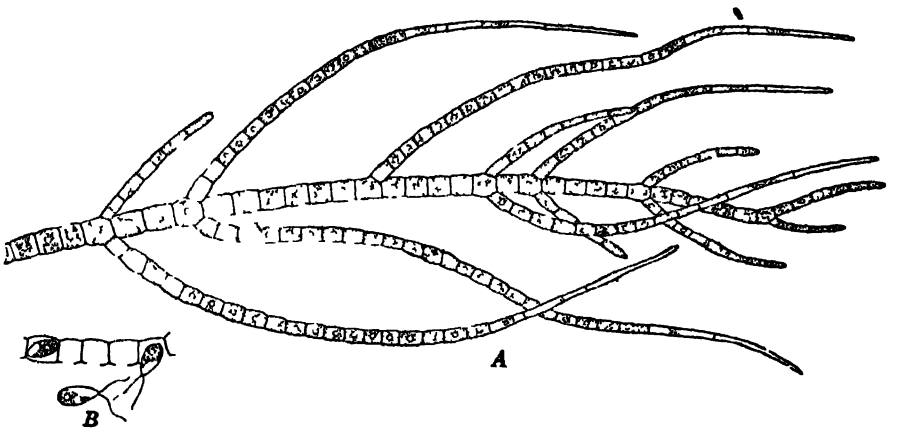


FIG. 18.—*A*, vegetative branch of *Stigeoclonium lubricum* (Dillw.) Kutz. *B*, zoospores of *S tenue* (C. A. Ag.) Kutz. (× 400.)

Stigeoclonium may develop pseudoparenchymatous *Palmella* stages, and it has been shown[1] that development of them may be induced by an increase in the osmotic pressure of the water or by the addition of small amounts of various toxic substances.

Cells of both the filamentous and palmelloid stages are uninucleate and have a single chloroplast. Larger cells of a filament have a transversely zonate chloroplast with several pyrenoids; smaller cells have the chloroplast extending the whole length of the cell and usually containing a single pyrenoid.

Vegetative multiplication by fragmentation may take place, but fragments from the erect branching portion do not grow vigorously when severed from the prostrate portion. Zoospore formation takes place quite readily in *Stigeoclonium*, and one usually finds all cells in the smaller branches sporulating the day after a collection is brought into the laboratory. The zoospores are quadriflagellate. In some species they are all the same size; in other species there are macro- and microzoospores.[2]

[1] Livingston, 1900, 1905. [2] Pascher, 1907.

Zoospores are generally formed singly within a cell and development of their flagella is due[1] to a blepharoplast-rhizoplast-centriole type of neuromotor apparatus. A zoospore swarms for a time and then comes to rest with its anterior pole downward. According to the species, the one-celled germling either grows into a short vertical filament that later develops the procumbent portion of a thallus, or it grows into a prostrate branching system from which erect branches arise.[2] Cases are also known where the macrozoospores are metamorphosed into rhizopodal stages that remain amoeboid for some time before they develop into filaments.[3] Aplanospores are generally formed singly within a cell and usually in several successive cells. Akinetes are sometimes formed in abundance.[4]

Sexual reproduction is usually by a fusion of biflagellate gametes of equal size (Fig. 18*B*), but a fusion of quadriflagellate gametes has been recorded[5] for certain species. The frequent failure of gametes to fuse with one another is probably due to the fact that the species is heterothallic. Gametes that have not fused to form a zygote usually develop parthenogenetically into filaments. The zygotes are spherical, are smooth walled, and germinate to form zoospores.

FAMILY 5. PROTOCOCCACEAE

The Protococcaceae may be unicellular, or multicellular and with the cells united in small packets. The chloroplasts are parietal and irregular in outline. There is no production of motile zooids.

The Protococcaceae include certain aerial fresh-water algae in which the cells are usually unicellular but in which there may be a vegetative division to form small packet-shaped colonies. The literature dealing with these algae is a mass of contradictions and phycologists are not even in agreement as to whether the best-known genus should be called *Protococcus* or *Pleurococcus*. Part of this confusion is due to the fact that every unicellular globose aerial green alga has been considered a species of *Protococcus*. The situation has improved in recent years with the growing realization that species in which the cells do not divide vegetatively belong to the Chlorococcales. Furthermore, there is very strong evidence that the true Protococcaceae never produce zooids and that any zoosporic unicellular green alga belongs to the Chlorococcales rather than to the Protococcaceae. The nonzoosporic unicellular aerial algae appear to be reduced forms derived from a branching filamentous ancestor. Sometimes there may be a reversion toward the ancestral condition, and, when growing under conditions of excessive moisture, *Protococcus* may

[1] Reich, 1926. [2] Fritsch, 1903; Strøm, 1921. [3] Pascher, 1915.
[4] Tilden, 1896. [5] Pascher, 1907.

form colonies of 50 or more cells and one in which certain of the cells are in definite but very irregular filaments.[1]

Solitary cells of *Protococcus* (Fig. 19) are spherical to ellipsoidal and with a fairly thick wall that is without a gelatinous envelope. Packets of two or more cells may be formed by a division of solitary cells. The first division is transverse; if further divisions take place, the plane of division is at right angles to the preceding one. Mutually apposed faces of daughter cells remain flattened for a time after cell division, but they eventually become rounded as the cells grow older and increase in size. A cell of *Protococcus* is uninucleate and solidly packed with cytoplasm. The peripheral portion of the cytoplasm is differentiated into a single

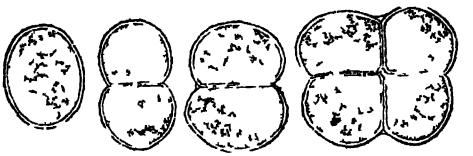


FIG. 19.—*Protococcus viridis* (After Age (×1,300)

laminate chloroplast with more or less lobed margins. Sometimes the chloroplast is so greatly lobed that there appear to be two or more of them. Chloroplasts of *Protococcus* are usually without pyrenoids.

Cell division is the only known method of reproduction. The two daughter cells may remain apposed for a considerable time, or they may separate from each other and become spherical.

FAMILY 6. COLEOCHAETACEAE

The Coleochaetaceae may have the cells united in branching filaments of various form or may have solitary cells. The cells are uninucleate and have a single, laminate, parietal chloroplast. All or certain cells in a thallus may bear one or more setae with a central filament of cytoplasm and a sheath of gelatinous material partially or completely enclosing the cytoplasmic filament. Most genera of the family produce zoospores. Sexual reproduction may be isogamous or oogamous.

The family includes about 10 genera and 25 species, almost all of them fresh-water in habit.

Colcochaete, with about 10 species, is a fresh-water aquatic that usually grows epiphytically upon other algae or upon submerged angiosperms, but may grow endophytically within cell walls of Charales. The cells are joined end to end in branching filaments, some of which may be prostrate and others erect (Fig. 20*B*); or all branches may be prostrate and either distinct from one another or laterally apposed to form

[1] Chodat, 1909; Snow, 1899.

a pseudoparenchymatous disk (Fig. 20*A*). In all of these thalli certain cells bear a single long unbranched cytoplasmic seta whose base is ensheathed by a cylinder of gelatinous material. The development of a seta is due to a blepharoplast that lies immediately beneath a small pore in the cell wall.[1] Cells of *Coleochaete* are uninucleate and with a single

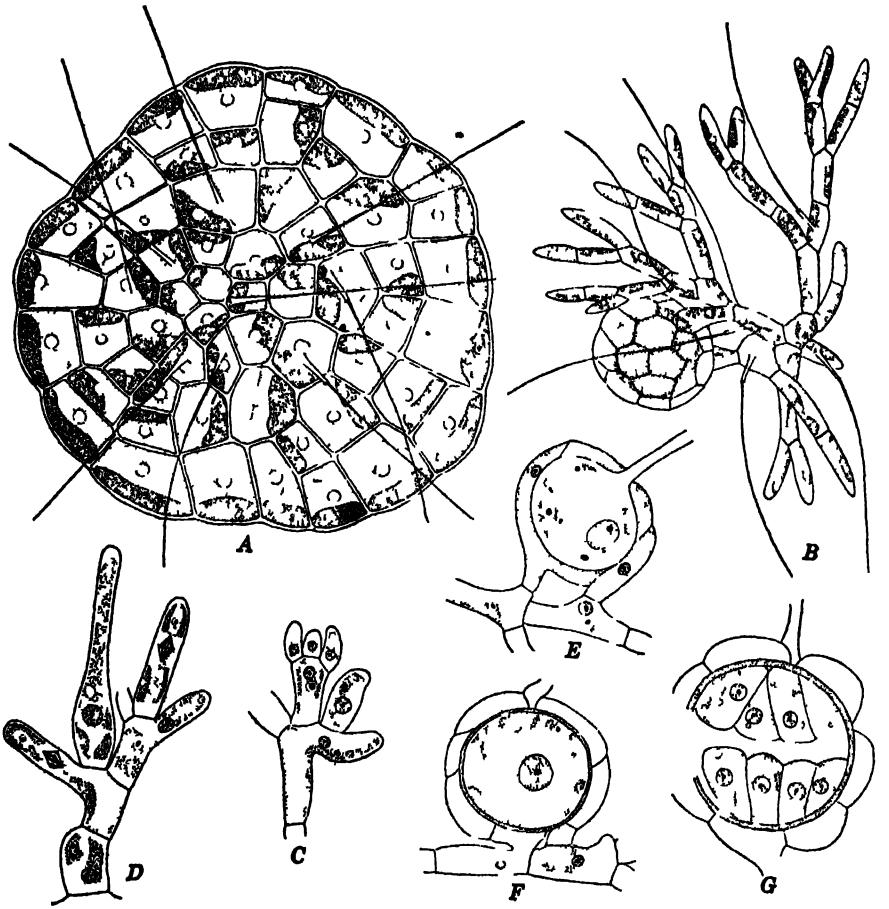


FIG 20.—*A*, *Coleochaete scutata* Bréb (× 375) *B G*, *C. pulvinata* A Br *B*, vegetative branch with a spermocarp (× 110). *C*, antheridia *D*, oogonium *E F*, young spermocarps *G*, germinating spermocarp (*C–G*, *after Oltmanns*, 1898)

laminate chloroplast that partially or wholly encircles the protoplast. There is usually one large pyrenoid within a chloroplast.

Asexual reproduction is by means of biflagellate zoospores that are formed singly within a cell. Isolated cells of a thallus may produce zoospores at any time of the year, but in the spring there is frequently a production of zoospores by every cell in a plant living over from the

[1] Wesley, 1928.

previous summer. A zoospore escapes by moving in an amoeboid manner through a pore in the parent-cell wall and then swarms for an hour or so before it comes to rest and secretes a wall.[1] The one-celled germling soon begins to develop into a multicellular thallus, and, when a developing thallus consists of but a few cells only, the cellular arrangement is that characteristic of the species. One or more cells of young developmental stages bear setae. Aplanospores with fairly thick walls may also be developed singly within a cell.[2]

Most species of *Coleochaete* reproduce sexually, although there are dwarf species that form zoospores only.[3] Sexual reproduction is oögamous, and, according to the species, the plants are heterothallic or homothallic. In *C. pulvinata* A. Br.[4] and *C. Nitellarum* Jost[5] the antheridia are bluntly conical and are usually borne at the tips of branches (Fig. 20*C*). Antheridia of *C. scutata* Bréb. are developed midway between center and periphery of the discoid thallus.[6] In this species a vegetative cell divides into two daughter cells, one of which, the antheridial mother cell, redivides to form antheridia. Antheridia of *Coleochaete* each produce a single biflagellate antherozoid which may be green or colorless. Oogonia of *C. pulvinata* are formed by a metamorphosis of one-celled lateral branchlets (Fig. 20*D*). The oogonium of this species[4] is a flask-shaped structure with a long colorless neck, the *trichogyne*. Oögonia of *C. scutata* have an inconspicuous trichogyne. They are formed from marginal cells of a thallus. Marginal growth of *C. scutata* continues after differentiation of the oogonia so that they, with their contained zygotes, eventually come to lie some distance in from the thallus margin.

Fertilization takes place by an antherozoid swimming into an oögonium and there uniting with the egg. The zygote remains within the oögonium, secretes a thick wall, and increases greatly in size. At the same time there is an upgrowth of branches from the cell below the oögonium and from neighboring cells to form a parenchymatous layer that more or less completely encloses the oogonium (Fig. 20*E–F*). The oogonium with its ensheathing layer of cells, which soon become reddish brown, is termed a *spermocarp*. The spermocarps remain dormant over winter.[6] The gametes uniting to form a zygote have nuclei of quite different size. But the male gamete nucleus increases greatly in size as it approaches the female nucleus, and, when the two fuse, they are of approximately the same size.[5] Division of the zygote nucleus is reductional,[7] and each series of nuclear division is followed by a cytokinesis effected by means of a cell plate. Division continues until there are 8 to 32 daughter protoplasts (Fig. 20*G*), and then each of them is meta-

[1] Lambert, 1910; Pringsheim, 1860; Wesley, 1930. [2] Wesley, 1928.
[3] Lambert, 1910. [4] Oltmanns, 1898. [5] Lewis, 1907. [6] Wesley, 1930.
[7] Allen, 1905.

morphosed into a biflagellate zoospore.[1] The zoospores are liberated by a breaking of the spermocarpic and zygote walls. The liberated zoospores swarm for a short time and then come to rest and develop directly into new thalli.

FAMILY 7. TRENTEPOHLIACEAE

The Trentepohliaceae have their cells united in irregularly branched filaments with a loose or a compact branching. The protoplasts may contain one or several chloroplasts and are always uninucleate when young. Zoospores are formed in sporangia differing in shape from vegetative cells. Several genera form biflagellate isogametes within gametangia resembling sporangia.

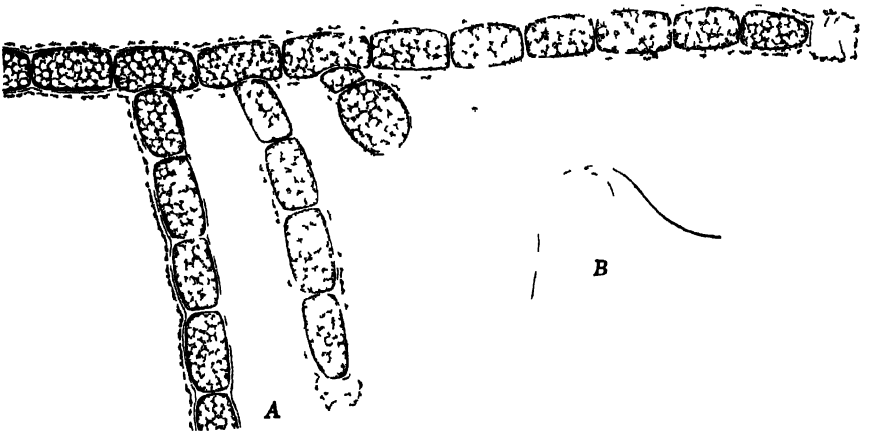


FIG. 21.—*Trentepohlia aurea* var *polycarpa* (Nees and Mont.) Hariot. *A*, portion of a thallus with a sporangium on one branch. *B*, zoospore. (*A*, × 325, *B*, × 975.)

The family includes some 18 genera and 80 species, a large majority of which are fresh-water in habit.

Typical members of the family, as *Trentepohlia*, have reproductive cells markedly different from vegetative cells, but there are genera in which differences between the two are so slight that it is a question whether they belong to the Trentepohliaceae or to the Chaetophoraceae.

Trentepohlia, with more than 50 species, is a strictly aerial alga in which the thallus is filamentous and branched (Fig. 21*A*). It is especially abundant in the tropics, but several species grow in temperate and subarctic regions. The alga grows in a felted layer on rocks and on the leaves and bark of trees. The plant mass is yellowish red to brownish red and quite conspicuous. Sometimes, as on the Monterey Peninsula, California, the alga grows in sufficient abundance to affect the color of the landscape.

[1] Chodat, 1898; Oltmanns, 1898; Pringsheim, 1860.

The major portion of the plant body may be prostrate and have very short erect branches, or the erect portion may be more extensive than the prostrate portion. Branching of the erect portion may be predominately alternate, opposite, or unilateral. The cells are cylindrical to moniliform and rarely with a length more than twice the breadth. They have lamellated walls composed almost entirely of cellulose.[1] Some species have the wall layers parallel to one another and encircling the cell; other species have the wall layers outwardly and upwardly divergent. In the latter type of wall there is usually a cap of pectose on the terminal cell of each branch. These caps, which are composed of successive transverse lamellae, may become so cumbersome that they impede apical growth of a branch.[1]

The protoplasts are uninucleate, when the cells are young, but may become multinucleate in old cells. There are several parietal chloroplasts in each cell, and, according to the species, they may be disks, spiral bands, or combinations of the two.[2] Usually, however, the number and structure of the chloroplasts are completely obscured by a haematochrome which colors the entire protoplast a deep orange-red. It has been thought that the haematochrome serves as a light screen, but there is an equal possibility[2] that it serves as a reserve food supplemental to the starch.

Asexual reproduction is by means of zoospores which are formed within terminal or intercalary sporangia. All intercalary and some terminal sporangia are without concentric rings of wall material where they abut on vegetative cells. Such sporangia are sessile and never become detached from the thallus. Liberation of their zoospores takes place within a few minutes after a plant is moistened, and the zoospores escape through a lateral pore in the sporangial wall. Some species with terminal sporangia have them borne upon basidium-like vegetative cells or have successive funnel-shaped layers of wall material separating them from vegetative cells.[3] Such sporangia are readily detachable and are dispersed as wind-borne spore-like bodies that immediately produce zoospores when moistened.[4] Zoospores from sessile sporangia are always biflagellate (Fig. 21*B*); those from detachable sporangia may be quadriflagellate.[5] Under certain conditions the contents of a sporangium may develop into aplanospores instead of into zoospores. Vegetative cells, especially those in the prostrate portion, may develop into thick-walled akinetes. The akinetes germinate directly into new filaments.[5]

There are a few records[6] of a fusion of biflagellate gametes that are produced in gametangia identical in appearance with stalked sporangia.

[1] West and Hood, 1911. [2] Geitler, 1923. [3] Brand, 1910.
[4] Gobi, 1871; Karsten, 1891. [5] Meyer, K., 1909.
[6] Meyer, K., 1909; Wille, 1887.

Possibly all reproductive cells producing biflagellate zooids are gametangial in nature, and the failure of biflagellate swarmers to fuse in pairs may be due to the fact that *Trentepohlia* is heterothallic.

ORDER 4. ULVALES

The Ulvales have uninucleate cells that divide in two or in three planes to produce a parenchymatous thallus that may be an expanded sheet, a hollow tube, or a solid cylinder. Asexual reproduction is by means of quadriflagellate zoospores. Sexual reproduction is isogamous or anisogamous and by means of biflagellate gametes.

The order includes 5 or 6 genera and about 110 species. A majority of the species are marine, but certain of them grow in brackish or in fresh water.

The cell structure is similar to that of Ulotrichales, and many phycologists think that differences in vegetative organization are not fundamental enough to warrant segregation from the Ulotrichales. In any case, the genera referred to the Ulvaceae are universally recognized as forming a natural family. *Ulva* and one other genus (*Enteromorpha*) have been shown[1] to be diplohaplontic and to have the two generations identical in form and structure.

The order is divided into two families.

FAMILY 1. ULVACEAE

The Ulvaceae have a thallus which is an expanded sheet one or two cells in thickness, a hollow cylinder with a wall one cell in thickness, or a strip two or more cells broad. The cells are uninucleate and with a single, parietal, more or less laminate chloroplast. Asexual reproduction is by means of quadriflagellate zoospores, and in two genera they germinate to form a haploid plant that produces biflagellate gametes only.

There are 4 or 5 genera and about 105 species. Most species are strictly marine, but some may also grow in brackish or fresh water, and a few others are strictly fresh-water.

Ulva, the sea lettuce, has about 30 species, all marine, but a few of them also grow in brackish water. *Ulva* is a common alga of the midtidal zone. It frequently grows in great profusion in waters polluted by sewage.

The thallus is an expanded sheet (Fig. 22*A*) two cells in thickness and is attached to the substratum by a holdfast composed of rhizoidal outgrowths from the lower cells. When seen in cross section, the cells are isodiametric or vertically elongate to the thallus surface (Fig. 22*B*). Their walls are more or less confluent with one another to form a tough gelatinous matrix. Each cell contains a single laminate to cup-shaped

[1] Bliding, 1933; Föyn, 1929, 1934*A*; Hartmann, 1929; Ramanthan, 1936.

chloroplast that lies next to the outer face of the cell. The chloroplast contains a single pyrenoid. The cells are uninucleate and with the nucleus variously located in the interior half of the cell. Cell division

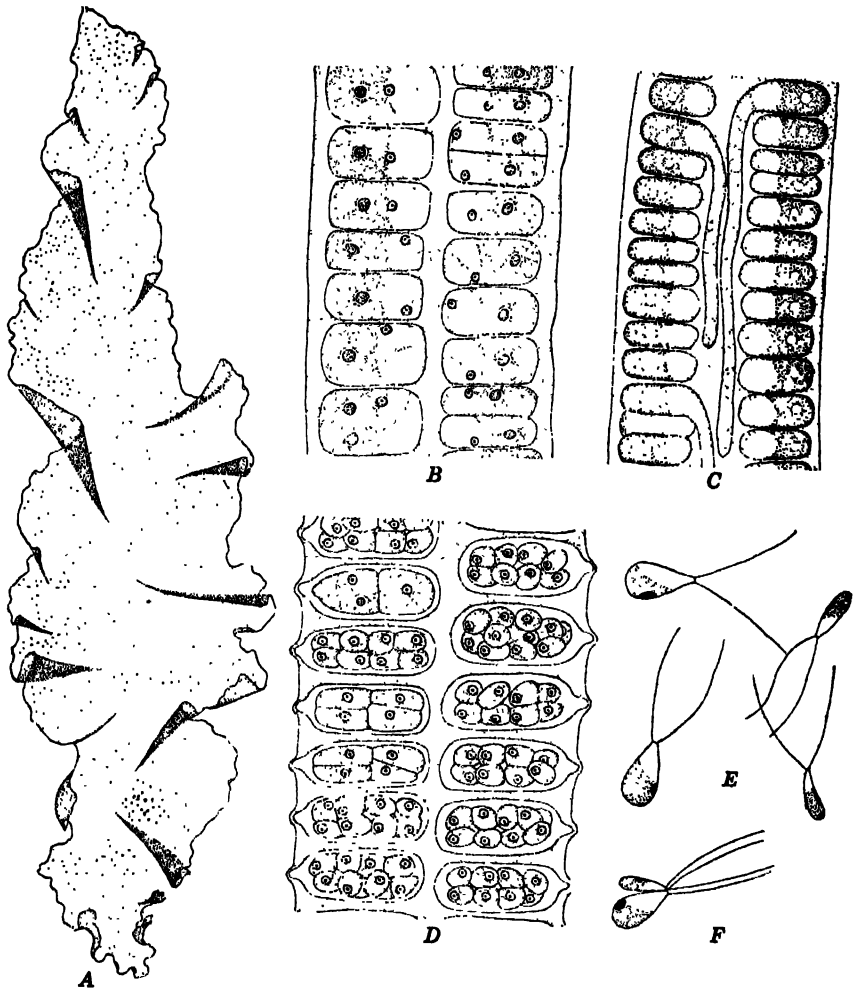


FIG. 22.—*A*, thallus of *Ulva stenophylla* Setchell and Gardner. *B F*, *U. lobata* (Kütz.) S and G. *B*, vertical section through upper portion of a thallus. *C*, same through basal portion. *D*, gamete formation. *E*, gametes. *F*, gametic union. (*A*, × ½; *B*, *D*, × 975; *C*, 650; *E–F*. × 1,300.)

may occur anywhere in a thallus, but all divisions are in a plane perpendicular to the thallus surface.

Certain cells in the lower portion of a thallus send out long colorless rhizoids (Fig. 22*C*) that grow down between the two layers of cells and intertwine freely with one another. Near the point of attachment to the substratum, they emerge from the thallus and become closely appressed

to one another to form a pseudoparenchymatous holdfast. Emergent portions of rhizoids are transversely septate and multinucleate and contain chlorophyll. The holdfast portion of a thallus is perennial and proliferates new blades each spring.[1]

When *Ulva* is growing in quiet waters of estuaries, it may multiply by growth of fragments accidentally detached from a thallus. There is but little vegetative multiplication among individuals growing in the open ocean.

Ulva has an alternation of generations in which quadriflagellate zoospores from diploid plants germinate to form haploid plants that produce biflagellate gametes. The haploid and diploid generations are identical. Zoospores may be formed in any cell of the sporophyte, with the exception of the lowermost ones. The first cells to produce zoospores are those near the thallus margin; later on, cells more remote from the margin produce zoospores, and spore production continues until nothing remains of the blade but a filmy mass of empty cell walls. The formation of zoospores is identical with that of gametes except that division of the nucleus is reductional.[2] The zoospores are liberated through a pore in the parent-cell wall and usually swarm only for a few minutes before coming to rest and secreting a wall. The first cell division in growth of the new generation is transverse, the lower cell developing into a rhizoidal holdfast and the upper into the blade. The upper cell divides transversely to form a filament of a few cells after which cell divisions are both vertical and transverse.[3]

Gametes are formed by a repeated bipartition of the protoplast of a cell. In *U. lobata* (Kutz.) Setchell and Gardner the first cleavage is always parallel to the thallus surface and the second in a plane perpendicular to the first (Fig. 22*D*). The pyrenoid persists in one daughter protoplast of the first cleavage but usually disappears before the second cleavage takes place. Cleavage continues until there are 16 or 32 daughter protoplasts, and then each of them is metamorphosed into a biflagellate gamete. In *U. lobata,* and probably in other species, a cell about to cleave develops a beak-like outgrowth on its outer face that extends to the thallus surface. This eventually becomes the pore through which the gametes are liberated. Species of *Ulva* growing along the coast of California discharge their gametes when they are reflooded by the incoming tide. Gamete discharge is profuse during the low spring tides of each lunar month, and such discharges are often liberated in sufficient quantity to color the water green. The biflagellate gametes are pyriform, with a single chloroplast, and with a conspicuous eyespot (Fig. 22*E*). Many, if not all, species are heteromallic, and in one species

[1] Delf, 1912. [2] Foyn, 1929, 1934*A*. [3] Schiller, 1907.

it has been shown[1] that there is a genotypic determination of sex at the time zoospores are formed. Fusing gametes are usually of equal size,[2] but one Pacific Coast species, probably *U. lobata*, seems to be anisogamous (Fig. 22*F*). The quadriflagellate zygote swarms for a short time and then comes to rest, loses its flagella, and secretes a wall. Germination follows within a day or two and division of the zygote nucleus is equational.[3] Development of germlings from zygotes is similar to that of germlings from zoospores. There may also be a parthenogenetic development of thalli from gametes.[1] Such thalli are haploid and produce gametes.

FAMILY 2. SCHIZOMERIDACEAE

Mature thalli of Schizomeridaceae are solid cylinders several cells in diameter. There is but one genus, *Schizomeris*. It is a fresh-water alga with two or three species.

Some phycologists[4] hold that *Schizomeris* is merely a developmental form of *Ulothrix* and unworthy of generic recognition; others[5] hold that it is a valid genus and one belonging to the Ulotrichaceae. During recent years there has been a growing tendency[6] to accept the suggestion[7] that its affinities are more with the Ulvales than with the Ulotrichales. It is thought to differ from Ulotrichales because cell division is in three planes (not one) and because the method of escape of zooids is quite unlike that of Ulotrichales.

During the early stages of development, a thallus of *Schizomeris* is an unbranched uniseriate filament with an acuminate distal cell and a somewhat elongate basal cell terminating in a discoid holdfast. Later on in its development there may be vertical divisions at right angles to each other in all cells except those toward the base. Continued division results in a thallus that is a solid cylinder of brick-like cells (Fig. 23). The cylinder may have parallel sides, or it may be constricted at infrequent and irregular intervals. Cells of simple filaments of *Schizomeris* have fairly thick lateral walls and are separated from one another by "ring-like" transverse walls.[8] These rings persist after vertical division begins, and they separate portions of the cylindrical thallus derived from a single cell of the filamentous stage. Chloroplasts of the filamentous stage are ulotrichoid and encircle about two-thirds of the protoplast. They usually contain several pyrenoids. A cell of the cylindrical portion of a thallus has a more massive chloroplast, which fills most of the protoplast. In one species[9] the chloroplasts in cells of older thalli may be

[1] Foyn, 1934*A*. [2] Foyn, 1934*A*; Schiller, 1907. [3] Foyn, 1929, 1934*A*.
[4] Printz, 1927. [5] Collins, 1909; Heering, 1914.
[6] Korshikov, 1927; West, G. S., 1916. [7] Hazen, 1902.
[8] Watson and Tilden, 1930. [9] Fritsch and Rich, 1924.

greatly lobed and have several pyrenoids or be broken up into several chloroplasts, each with a single pyrenoid.

Vegetative multiplication may take place by a fragmentation of old thalli. The region at which a break occurs is almost always a constricted portion of a thallus, and fragmentation may be due to a disintegration of the transverse ring of wall material persisting from the filamentous stage. Asexual reproduction is by means of quadriflagellate zoospores formed by cells in the upper part of a thallus. Most[1] of those who have observed the liberation of zoospores record a breaking down of cross walls in the region of zoospore formation and an escape of zoospores



FIG. 23.—*Schizomeris Leibleinii* Kütz. Portions of a thallus at three different levels. (× 325.)

through the thallus apex, but a liberation of zoospores by a gelatinization of the lateral walls has also been reported.[2]

ORDER 5. SCHIZOGONIALES

Thalli of Schizogoniales may be filamentous, plate-like, or solid cylinders. They are composed of uninucleate cells with a single stellate chloroplast. No zoospores are formed by members of this order, and there is no sexual reproduction. Reproduction is by means of aplanospores and akinetes.

There are 2 or 3 genera and about 25 species; some fresh-water, others marine.

There is but one family, the Schizogoniaceae. The systematic position of this family is controversial. Some phycologists[3] place it in a separate order; others[4] hold that it does not merit ordinal rank. The shape and position of the chloroplasts and the multiple files of akinetes of *Prasiola* suggest that the affinities are with *Porphyra* (page 302) rather than with the Chlorophyceae. It has even been intimated[5] that the two

[1] Hazen, 1902; Wolle, 1887; Wood, 1872. [2] Korshikov, 1927.
[3] Setchell and Gardner, 1920; Smith, G. M., 1933; West, 1916.
[4] Fritsch, 1935; Printz, 1927. [5] Setchell and Gardner, 1920.

types of akinetes found in certain species of *Prasiola* are antheridia and a simple type of cystocarp. Although there are these superficial morphological resemblances to *Porphyra*, there is a fundamental difference in the composition of pigments in Bangiales and in Schizogoniaceae.[1]

Some of the 20 or more species of *Prasiola* are marine and some are fresh water. Certain species grow only where the substratum is rich in soluble nitrogenous compounds, and most of the marine species are restricted to the spray zone of rocks covered with the droppings of sea birds.

Adult thalli of *Prasiola* are expanded sheets one cell in thickness and with the cells tending to lie in groups of four (Fig. 24 *A–B*). The tetrads may, in turn, lie in larger groups separated from one another by narrow or broad intervening spaces running in definite directions through a thallus. Attachment to the substratum may be by rhizoidal outgrowths from the thallus margin or by a thickened stipe. The first cell divisions in development of a thallus are always transverse and result in a simple filament. The filamentous stage may at times have a false branching as a result of death of one or two cells and a growth of the adjoining portions through the sheath investing the filament.[2] The juvenile condition may persist indefinitely, or, as a result of vertical and transverse division, a filament may become either a ribbon two to a few cells broad or an expanded sheet about as broad as long.

Cells of vigorously growing thalli have a single central stellate chloroplast with a pyrenoid at the center (Fig. 24*C*). The nature of the food reserves is in dispute; some[3] affirm that starch is formed, and others deny[4] its presence. The cells are uninucleate, with the nucleus excentric in position.[5]

Vegetative multiplication may take place at the filamentous or at the adult stage. Multiplication at the filamentous stage is by a fragmentation into segments containing one to four cells,[3] or by a dissociation into spherical cells which readily separate from one another.[6] Vegetative multiplication of adult thalli is by an abscission of small proliferous outgrowths.

Asexual reproduction is usually by means of akinetes. These may be formed by metamorphosis of a vegetative cell, or akinete formation may be preceded by vegetative divisions that make a thallus two cells in thickness in the region where they are to be formed. Portions of the thallus two cells in thickness may have a direct development of the cells into akinetes[7] or may have the cells dividing into four daughter cells that become akinetes.[8] The akinetes are liberated by a softening of the thallus

[1] Kylin, 1930. [2] Brand, 1914; Gay, 1891; Wille, 1901.
[3] Gay, 1891; Wille, 1901. [4] Brand, 1914. [5] Wille, 1901.
[6] Borzi, 1895; Gay, 1891. [7] Setchell and Gardner, 1920. [8] Lagerheim, 1892.

matrix. They may develop directly into new plants, or they may become aplanosporangia which contain several aplanospores.[1]



FIG 24.—*A–B*, *Prasiola mexicana* J G Ag *A*, thallus *B*, portion of a thallus. *C*, vegetative cells of *P meridionalis* Setchell and Gardner. (*A*, × ½, *B*, × 485, *C*, × 975)

The recently described[2] anisogamous sexual reproduction by means of biflagellate gametes is in need of confirmation before it can be accepted

ORDER 6. CLADOPHORALES

The Cladophorales are multicellular and with the cells united end to end in simple or branching filaments. The cells are always multinucleate and have numerous discoid chloroplasts that may be free from one another or united by strands. Asexual reproduction is by means of zoospores, aplanospores, and akinetes Sexual reproduction is isogamous or oogamous.

The order includes about 12 genera and 340 species, some marine, others fresh-water.

The coenocytic multicellular Chlorophyceae in which the cells divide vegetatively are usually considered permanently septate Siphonales and placed in a single order, the Siphonocladiales. Certain of the families assigned to the Siphonocladiales have undoubtedly been derived from the Siphonales (page 122). However, as suggested by Fritsch,[3] the Cladophoraceae and Sphaeropleaceae appear to have been derived from the Ulotrichales rather than from the Siphonales. At first he thought they were sufficiently related to Ulotrichales to be considered a suborder;[3] later he thought[4] that the Cladophoraceae should be placed in a separate order. The systematic position of the Sphaeropleaceae is doubtful, and there are equally good arguments for retaining them among the Ulotrichales or transferring them to the Cladophorales.

Three genera of the Cladophoraceae have been shown to be diplohaplontic. In two of the genera[5] there is an alternation of identical

[1] Wille, 1901, 1906. [2] Yabe, 1932. [3] West and Fritsch, 1927.
[4] Fritsch, 1935
[5] Foyn, 1929, 1934; Hartmann, 1929; Schussnig, 1928, 1930*B*, 1931.

haploid and diploid generations. In the third genus (*Urospora*) there is[1] an alternation of a many-celled filamentous haploid generation with a coenocytic one-celled diploid generation.

The two families of the Cladophorales differ from each other in structure of vegetative cells and in the type of sexual reproduction.

FAMILY 1. CLADOPHORACEAE

The Cladophoraceae have multinucleate cylindrical cells in which the length is rarely more than eight times the breadth and in which the chloroplasts are not in distinct transverse bands. The cells are joined end to end in simple or in branched filaments. Asexual reproduction of most genera is by means of zoospores, but one genus produces akinetes only. Sexual reproduction is isogamous, by a fusion of biflagellate gametes.

There are about 11 genera and 340 species. Some genera are exclusively marine, some are exclusively fresh-water, and some have both marine and fresh-water species.

Cladophora, with some 160 species, is unusual in that it is widely distributed in both fresh and salt waters. The cylindrical cells have a length 3 to 20 times the breadth and are united end to end in freely branched filaments (Fig. 25*A*). The branching is usually lateral but often appears to be dichotomous because of the pushing aside (evection)[2] of the original axis of the branch. Branches originate as lateral outgrowths from the upper end of a cell and are usually formed only from cells near the end of a filament. The first cross wall formed in a branch is laid down close to the point of origin of the outgrowth. Thalli of *Cladophora* are usually sessile and attached to the substratum by fairly long rhizoidal branches, some of which arise adventitiously from cells near the base of a thallus. Certain of the rhizoidal branches develop short thick cells from which grow bushy short-celled branches.[3] Many species of *Cladophora* are perennial, the thallus dying back to the prostrate rhizoidal system whose cells are filled with food reserves. In the following growing season certain of these cells give rise to new erect branches.

The cells have thick stratified walls consisting of an inner cellulose zone, a median pectic zone, and an outer chitinous zone.[4] There is a fairly thick layer of cytoplasm internal to the wall, and, internal to this, there is usually one large central vacuole, but sometimes there are several vacuoles in the central portion of a protoplast. The chloroplast may be a reticulate sheet completely encircling the protoplast, with pyrenoids here and there in the reticulum; or there may be numerous discoid chloroplasts most of which lie next to the cell wall but a few of which may lie in cytoplasmic strands crossing the central vacuole. Only certain of the discoid

[1] Jorde, 1933. [2] Brand, 1901. [3] Brand, 1909. [4] Wurdack, 1923.

chloroplasts contain pyrenoids. The cells are always multinucleate and have the nuclei internal to the chloroplast or chloroplasts. The nuclei are relatively large and with a well-defined chromatin-linin network. Chromosomes formed during mitosis may be of different lengths or all the same length.[1] There is no distinct spindle during the division of nuclei, and the nuclear membrane persists until division is completed. Frequently the nucleolus is also persistent and is divided into two equal parts during mitosis.

All critically investigated species have been shown[2] to have an alternation of generations and a production of quadriflagellate zoospores by the

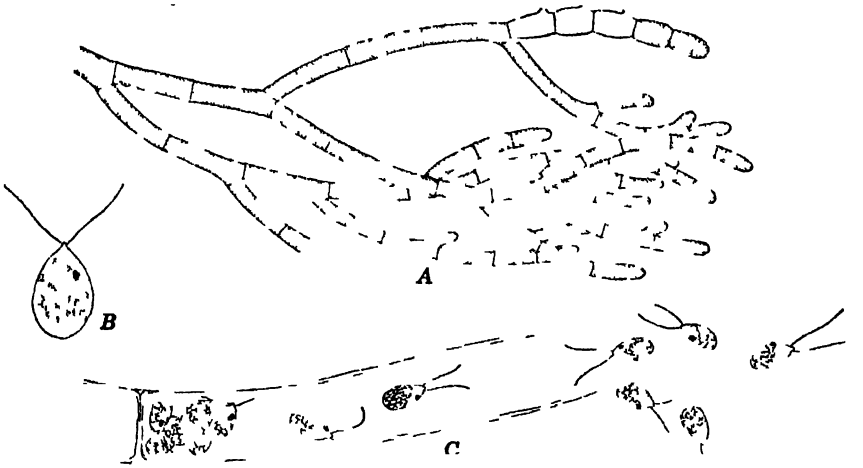


FIG. 25.—*A–B*, *Cladophora glomerata* (L.) Kutz. *A*, portion of a thallus. *B*, gamete. *C*, liberation of gametes of *C. Kuetzingianum* Grun. (*A*, × 40, *B*, × 600, *C*, × 325.)

diploid generation. The zoospores are usually formed only in vigorously growing cells near the tips of branches. There is a period of active nuclear division, and in certain species[3] these divisions have been shown to be reductional. *C. glomerata* (L.) Kutz. is atypical in that meiosis takes place just before formation of gametes.[4] After completion of the nuclear divisions, there is a progressive cleavage into uninucleate protoplasts by a progressive vacuolization.[5] Each uninucleate protoplast is metamorphosed into an ovoid quadriflagellate zoospore with an eyespot and chloroplasts. Coincident with the cytoplasmic cleavage, there is a development of a small lens-shaped area at or near the upper end of the cell wall. The gelatinization and dissolving of this area produces a small circular pore through which the zoospores escape singly. As a rule, all

[1] Carter, Nellie, 1919; Foyn, 1934; Schussnig, 1923, 1930*B*; T'Sercla.es, 1922.
[2] Foyn, 1929, 1934; Schussnig, 1928, 1930, 1931.
[3] Foyn, 1934; Schussnig, 1928, 1930*B*. [4] List, 1930.
[5] Czempyrek, 1930.

zoospores escape from a parent-cell wall, and one rarely finds zoospores remaining within a parent cell and there developing into aplanospores. Liberation of zoospores from marine species growing in the intertidal zone takes place when thalli are reflooded by the incoming tide. Germination takes place soon after the zoospores cease swarming. The one-celled germling elongates vertically, becomes multinucleate, and then divides transversely into two daughter cells, the lower of which is rhizoidal.

Cells of the erect branches of mature plants may develop into akinete-like structures, but these often divide to form new cells without becoming detached from the filament in which they are borne.[1]

Sexual reproduction is by means of biflagellate gametes formed in the same manner as are zoospores. They also escape singly from the parent cell and through a small lateral or terminal pore (Fig. 25*B*-*C*). In many cases they have the posterior pole forward as they move through the pore. Some species of *Cladophora* are heterothallic[2] and only have a union of gametes when the two have been produced by different plants. Certain heterothallic species have a disintegration of gametes which have not fused to form a zygote; others have a parthenogenetic germination of gametes that fail to fuse with one another.

The zygote germinates directly into a new plant without a period of rest. Division of the zygote nucleus and its daughter nuclei is equational. The diploid thallus resulting from germination of a zygote is an asexual plant and produces zoospores only.

FAMILY 2. SPHAEROPLEACEAE

The Sphaeropleaceae have cells with a length 15 to 60 times the breadth and have them united end to end in unbranched filaments. Chloroplasts within a cell lie in numerous transverse bands. There is no reproduction by zoospores or any other type of asexual spore. Sexual reproduction is oogamous.

The single genus, *Sphaeroplea*, is a fresh-water alga with five species. It is usually found on periodically inundated ground or in flooded meadows. In such places it may develop to maturity, fruit, and disappear within four or five weeks.

The lateral walls of a cell are relatively thin and have no gelatinous sheath. End walls separating the cells from one another are unevenly thickened and sometimes have knob-like projections. The protoplast contains numerous transverse biconcave septa of cytoplasm separated from one another by large vacuoles. Each cytoplasmic septum contains several nuclei and numerous discoid chloroplasts (Fig. 26*A*), certain of which contain pyrenoids.[3] Sometimes the chloroplasts in a septum are

[1] Cholnoky, 1930. [2] Foyn, 1929, 1934; Schussnig, 1930, 1930*A*, 1930*B*.
[3] Klebahn, 1899.

so densely crowded that they appear to be a single transverse band similar to the chloroplast of *Ulothrix*. There is a thin layer of cytoplasm between the vacuoles and the side walls of a cell, but it usually lacks chloroplasts. Here and there in the cell a septum develops a vacuole, the enlargement of which divides the septum into two equal parts that become more and more remote from each other as the vacuole increases in length. Elonga-

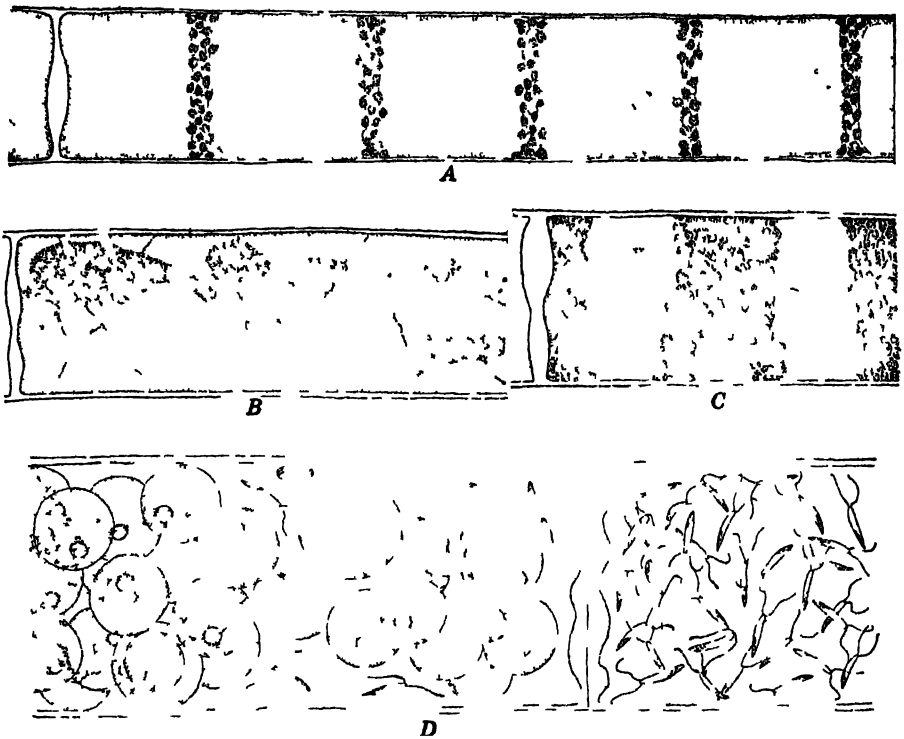


FIG 26.—*A*, portion of a vegetative cell of *Sphaeroplea annulina* (Roth) C. A. Ag. *B*, *D*, *S. cambrica* Fritsch. *B*, early stage in development of an antheridium. *C*, portion of an antheridium with protoplasm cleaved into small fragments. *D*, portion of an oogonium in which the eggs are being fertilized, and portion of an adjoining antheridium. (× 650.)

tion of a cell and the formation of new cytoplasmic septa do not continue indefinitely since sooner or later there is a formation of a transverse wall. Growth in length of a filament may continue indefinitely, but usually the filaments become accidentally severed before attaining a length of more than a few centimeters. Vegetative multiplication by an accidental breaking of filaments is the only method of asexual reproduction in *Sphaeroplea*.

Sexual reproduction is oogamous and differs from that of all other oogamous Chlorophyceae in that there is no change in shape of vegetative cells developing into oogonia or into antheridia. *Sphaeroplea* is the only

oögamous green alga in which more than one egg is formed within an oögonium. Every cell of a filament develops into a sex organ, and all filaments, at any given station, fruit at about the same time. Most species produce antheridia and oogonia in separate filaments, but sometimes the two are produced[1] in alternate cells of the same filament (Fig. 26*D*).

The first step in the formation of an antheridium is an increase in the number of nuclei in the protoplast and a division of the chloroplasts, accompanied by a disappearance of the pyrenoids.[2] There is then a clumping of the protoplast into a number of masses (Fig 26*B*) and a

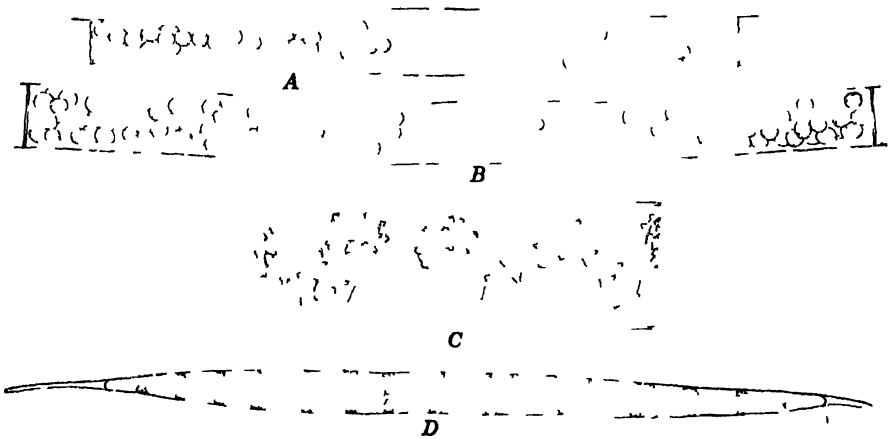


FIG. 27.—*A*, *B*, entire oogonia of *Sphaeroplea cambrica* Fritsch. *C–D*, *S. annulina* (Roth) C. A. Ag. *C*, zygotes. *D*, one-celled germling. (*A–B*, × 160, *C*, × 650, *D*, × 325.)

progressive cleavage of each mass into uninucleate protoplasts (Fig. 26*C*) that are metamorphosed into naked biflagellate spindle-shaped antherozoids.[3] The antherozoids escape singly through small pores in the lateral wall of an antheridium.

Cells developing into oogonia do not have an increase in the number of nuclei prior to cleavage of the cytoplasm into eggs. The eggs are multinucleate when first formed, but later there is a degeneration of all nuclei but one. This is not accompanied by a disappearance of the chloroplasts or pyrenoids.[4] The number and size of eggs within an oogonium are extremely variable, even in the same species. In most species the diameter of eggs is more than half that of an oogonium, and they lie in a single to double linear series within the oogonium. More rarely the eggs have a diameter less than a quarter that of an oogonium, and they lie in multiple longitudinal series (Fig. 27*A–B*). Oogonia containing mature eggs have small pores in their lateral walls; the anthero-

[1] Rauwenhoff, 1887; Smith, G. M., 1933.
[2] Klebahn, 1899.
[3] Golenkin, 1899; Klebahn, 1899.
[4] Gilbert, 1915; Klebahn, 1899.

zoids enter through these pores, swim about between the eggs, and eventually unite with them (Fig. 26*D*). In *S. tenuis* Fritsch fertilization probably takes place outside the oögonium, and there are reasons for thinking that both gametes of this species are motile.[1] Soon after fertilization, the zygote secretes a thick wall, with an ornamentation typical for the species, and the protoplast becomes brilliantly colored with haematochrome (Fig. 27*C*). The zygotes are eventually liberated by a decay of the oögonial wall, but they remain dormant for several months before germinating. They may remain viable for several years.

When germination takes place,[2] there is usually a division of the protoplast into four zoospores, but one, two, or eight zoospores are sometimes produced. The zoospores are biflagellate and ovoid when first liberated. Shortly before or after they cease swarming, they become spindle-shaped and have greatly attenuated poles. The protoplast of a zoospore secretes a wall after swarming ceases, but there is no formation of a holdfast. This free-floating cell increases to many times its original length and develops many transverse cytoplasmic septa before it divides transversely (Fig. 27*D*).

ORDER 7. OEDOGONIALES

The Oedogoniales have uninucleate cells seriately united in simple or branched filaments. Cell division is of a unique type and has a distinctive annular splitting of the lateral wall. Motile reproductive cells differ from those of most other Chlorophyceae in that they have a transverse whorl of flagella at the anterior end. Asexual reproduction is usually by means of zoospores but may be by means of akinetes. Sexual reproduction is always oögamous.

There are three genera and approximately 350 species, all fresh-water in habit.

The order is sometimes[3] placed in a separate subclass, the *Stephanokontae*, because of the distinctive zooids. The occurrence of stephanokontean zoospores in *Derbesia* (page 115), a genus far removed from the Oedogoniales, shows that this unusual type of zooid has been evolved in two independent phyletic lines of Chlorophyceae. Developing zooids of many other Chlorophyceae have a granule that divides to form two blepharoplasts, each of which forms a single flagellum (page 16). It has been suggested[4] that the stephanokontean swarmers of Oedogoniales and *Derbesia* have been evolved by an appearance of repeated divisions in the granule originally dividing to form two blepharoplasts. If this is true, there is good reason for thinking that the Oedogoniales are in the

[1] Fritsch, 1929.

[2] Cohn, 1856; Heinricher, 1883; Meyer, K., 1906; Rauwenhoff, 1887

[3] Blackman and Tansley, 1902; Tiffany, 1930; West, 1916. [4] Pascher, 1929.

same evolutionary line as the Ulotrichales. However, the Oedogoniales have evolved additional distinctive features besides a stephanokontean flagellation, especially a unique type of cell division and in certain species peculiar dwarf male filaments.

The three genera of the Oedogoniales are so closely related that they are placed in a single family, the Oedogoniaceae.

Oedogonium, with some 285 species, is the only genus with cells in unbranched filaments. It is always a submerged aquatic and is of frequent occurrence in permanent and semipermanent pools and ponds. The filaments may grow in extensive free-floating masses, or they may be epiphytic upon leaves and stems of submerged vascular plants or epiphytic upon the larger filamentous green algae. All species are sessile when young, and many of them remain sessile throughout their entire development. The basal cell is always modified to form a holdfast, and



FIG. 28.—Vegetative cell of *Oedogonium crassum* (Hass.) Wittr. (× 485.)

the distal cell is usually broadly rounded or acuminate. Intercalary cells of a filament have an apical-basal polarity, and this is maintained even if the filament breaks away and becomes free-floating.

The cells are cylindrical and with fairly thick rigid walls. Although the walls appear to be homogeneous in structure, all of them, except those of holdfasts,[1] consist of three concentric portions.[2] The portion next to the protoplast consists largely of cellulose, external to this is a zone of pectose, and the outermost portion has chitin as the predominating substance. Lateral walls of certain cells of every filament have one or more transverse striae at the distal end. They constitute the so-called *apical cap* (Fig. 28). The chloroplast is a reticulate sheet extending from pole to pole and completely encircling the protoplast. According to the species, the strands of the reticulum are broad or narrow, but in either case the majority of strands are parallel to the long axis of the cell. The pyrenoids, of which there are usually many in a chloroplast, lie at the intersections of the reticulum. Each pyrenoid is surrounded by a sheath of starch plates. Starch plates formed by the pyrenoids may migrate to, and accumulate in, the strands of the reticulum until the reticulate nature of the chloroplast is completely obscured by this "stroma" starch. The single nucleus usually lies midway between the ends of a

[1] Tiffany, 1924. [2] Wurdack, 1923.

protoplast and just within the chloroplast. It is of large size, is biscuit-shaped, has a well-defined chromatin-linin network and one or more nucleoli.[1]

Cell division is terminal or intercalary and may take place in any cell but the basal one. Prior to cell division, there is an upward migration of the nucleus until it lies about two-thirds the distance from the proximal end. After elongating somewhat, the nucleus divides mitotically. This generally takes place during the night. During the prophases of mitosis, there is an appearance of a ring of wall material that completely encircles

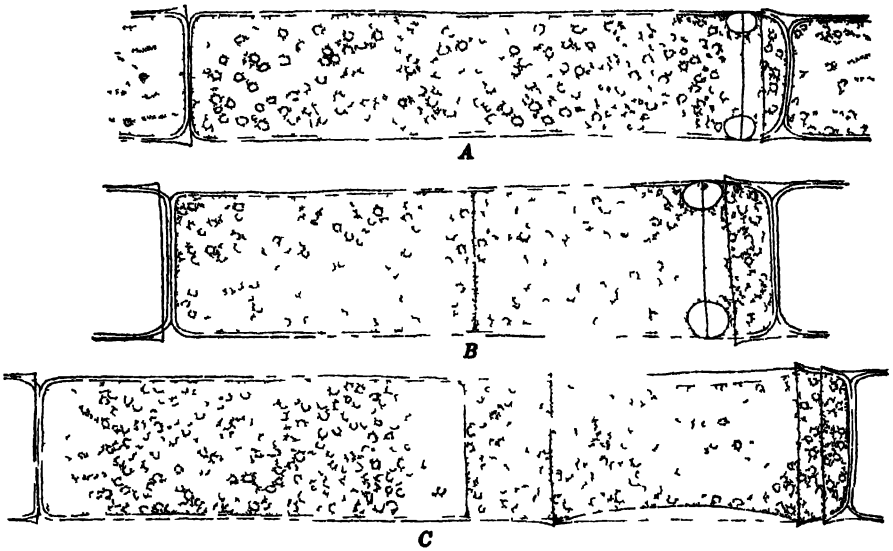


FIG. 29.– Cell division of *Oedogonium crassum* (Hass.) Wittr. (× 485)

the inner face of the lateral wall just below the distal end of the cell.[2] The ring, which is thought[3] to consist of hemicellulose, increases in thickness until it is several times thicker than the rest of the lateral wall (Fig 29*A*). There is next a formation of a small groove completely encircling the portion of the ring adjoining the lateral wall. A transverse rent then appears in the portion of the lateral wall external to the groove. Mitosis is completed by the time that the ring is fully developed, and, shortly after the two daughter nuclei are reconstructed, there is a transverse cytokinesis of the protoplast by an annular furrowing of the plasma membrane midway between the ends of the cell (Fig. 29*B*). There is no elongation of the cell during these stages of division, but, after transverse

[1] Kretschmer, 1930; Ohashi, 1930; Strasburger, 1880; Tuttle, 1910; van Wisselingh, 1908.

[2] Hirn, 1900; Kraskovits, 1905; Kretschmer, 1930; Ohashi, 1930; Pringsheim, 1858; Steinecke, 1929; Strasburger, 1880; Tuttle, 1910; van Wisselingh, 1908, 1908*A*.

[3] Steinecke, 1929

division of the protoplast, each daughter protoplast elongates to about the same length as that of the parent protoplast. This elongation takes but a short time and is often completed within 15 minutes. The lower daughter protoplast elongates until its distal end is level with, or slightly above, the former level of the hemicellulose ring. The wall lateral to this protoplast is therefore the side wall of the old parent cell. Meanwhile, the upper daughter protoplast has been elongating to about the same extent. The wall lateral to this protoplast is formed by a vertical stretching of the hemicellulose ring (Fig. 29*C*), except for the persistent portion

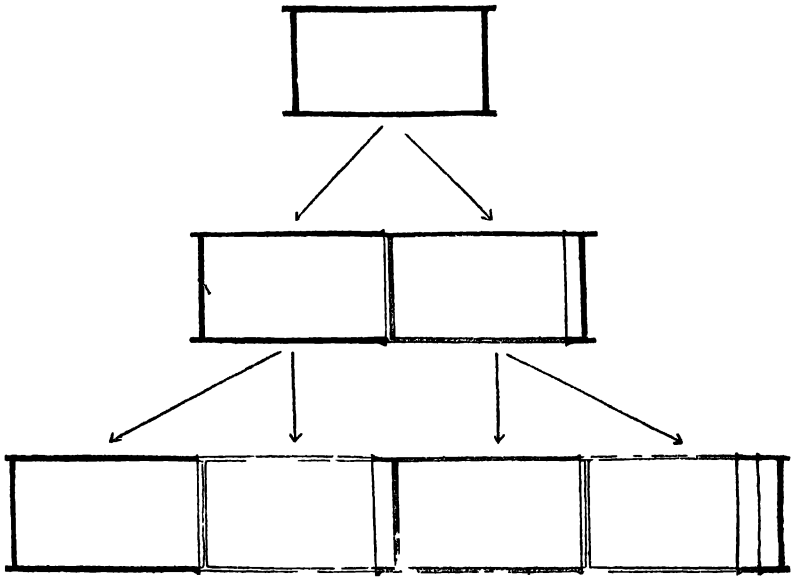


FIG 30 —Diagram showing the distribution of mother-cell walls to daughter cells in *Oedogonium* Walls of the first cell generation are shaded black those of the second generation are in stipple, and those of the third generation are unshaded

of the parent-cell wall at the upper end—the apical cap After the daughter protoplasts have completed their elongation, there is a secretion of a transverse wall which separates them from each other. Some phycologists describing cell division in *Oedogonium* hold[1] that the transverse wall is formed immediately after cytokinesis and that it is pushed upward as the lower daughter protoplast elongates.

Division of every cell in a filament and repeated division of the daughter cells would result in alternate cells with and without caps. Cells with one, two, three, and more caps would also have a definite disposition with respect to one another (Fig 30). This theoretical condition rarely obtains in nature, and frequently the repeated division of the distal daughter cell results in a filament in which a cell with several

[1] Strasburger, 1880

apical caps lies above several successive cells without caps. In some species the terminal cell is the only one with caps.

Vegetative multiplication by an accidental breaking of filaments is of common occurrence in certain species, especially those growing in free-floating masses. Permanently sessile species rarely multiply by fragmentation.

All species may produce zoospores, and their production is stimulated by an increase in the amount of carbon dioxide in the surrounding water.[1] Zoospores are formed singly within a cell and usually by cells containing abundant food reserves. Preparatory to zoospore formation, the nucleus retracts slightly from the chloroplast, and a hyaline region appears between the wall and nucleus.[2] A ring of blepharoplast granules appears about the margin of the hyaline area, and it is quite probable that each granule gives rise to one flagellum. Formation of the flagella is followed by a transverse splitting of the lateral wall at the apical cap, and the zoospore, surrounded by a delicate vesicle, emerges through the aperture (Fig. 31*A-C*). Liberation of zoospore and vesicle takes about 10 minutes. It has been thought[3] that the transverse splitting of the wall and the pushing out of zoospore and vesicle result from a pressure caused by an imbibitional swelling of gelatinous substances secreted by the protoplast. The vesicle surrounding a zoospore increases in size, but it soon disappears, and the zoospore swims freely in all directions. The period of swarming usually lasts but an hour or so, after which the zoospore comes to rest with the hyaline end downward, retracts its flagella, and develops a holdfast that attaches it to the substratum (Fig. 31*E*). The type of holdfast depends both upon the species concerned and upon the nature of the substratum. Species with a rhizoidal holdfast have been shown[4] to form a simple holdfast if the substratum is smooth and a more or less branched one if the substratum is rough. A zoospore secretes a wall shortly after it becomes sessile, but the wall differs from that enclosing other vegetative cells in that it lacks a superficial layer of chitinous material.[5]

Zoospores that have ceased swarming and have not become affixed to some object may develop a wall, but most of such one-celled germlings immediately form new zoospores.[6] Sessile one-celled germlings of most species divide transversely by means of an apical ring similar to that in an ordinary cell division.[7] Division of the distal cell and the division and redivision of its daughter cells result in a many-celled filament; the basal

[1] Gussewa, 1927, 1930.

[2] Gussewa, 1927, 1930; Hirn, 1900; Klebs, 1896; Kretschmer, 1930; Ohashi, 1930; Pringsheim, 1858; Strasburger, 1892.

[3] Steinecke, 1929 [4] Peirce and Randolph, 1905. [5] Tiffany, 1924.

[6] Fritsch, 1902; Wille, 1887*A*. [7] Hirn, 1900.

cell formed by the first division does not divide again (Fig. 31*F*). Sessile one-celled germlings of a few species are hemispherical and do not form a ring at the time of the first division Division of these germlings begins[1] with the protrusion of a cylindrical outgrowth from the upper portion. When the cylinder has attained a certain length, there is a transverse division of the protoplast at the juncture of cylinder and hemisphere and a formation of a cross wall between the two.

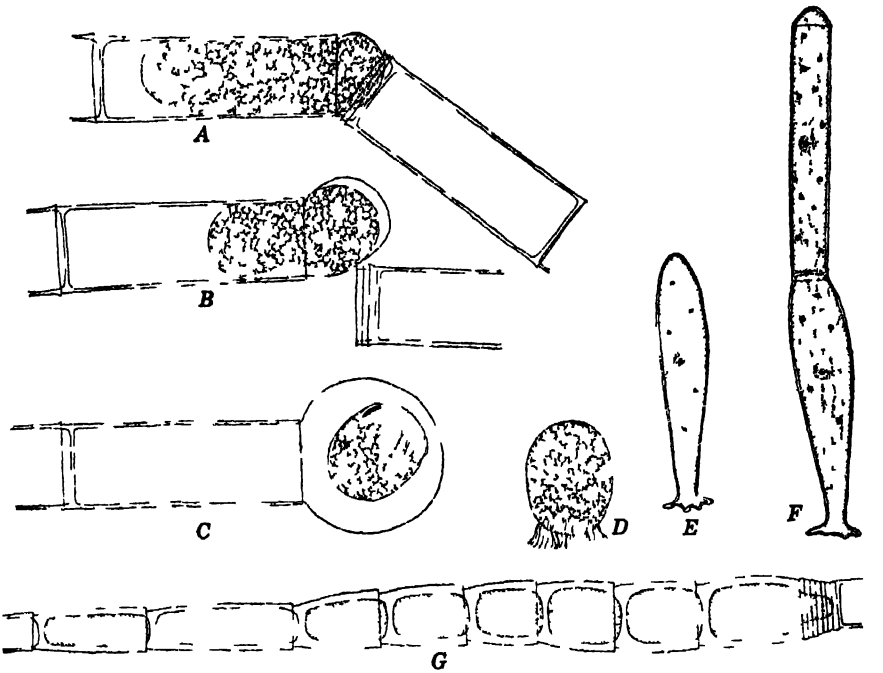


FIG 31 — *Oedogonium* spp 1 *C* liberation of zoospore *D*, zoospore *E F*, germlings. *G* akinetes (× 325)

Oedogonium may also form akinetes[2] They are formed in chains of 10 to 40 and in inflated cells resembling oogonia (Fig 31*G*) Their protoplasts are rich in reserve starch and a reddish-orange oil. Akinetes germinate directly into new filaments.

Sexual reproduction is oogamous. It is of frequent occurrence when filaments are growing in standing water but is infrequent if they are in flowing water.) Each species produces sex organs at rather definite seasons of the year. As a rule, species with small cells have a short vegetative phase and fruit early in the growing season, whereas those with large cells have a longer vegetative period and fruit later in the growing season.[3]

[1] Fritsch, 1904 [2] Wille, 1883 [3] Tiffany, 1930; Tiffany and Transeau, 1927.

Sexual reproduction may be *macrandrous*, with antheridia produced in filaments of normal size; or *nannandrous*, with the antheridia produced by special dwarf male filaments. Macrandrous species may be homothallic or heterothallic. Their antheridia are either terminal or intercalary and are produced by division of an *antheridial mother cell*. This division is quite similar to that of a vegetative cell, except that the upper cell, which is the *antheridium*, is much shorter than the sister cell.[1] The lower sister cell may, in turn, divide repeatedly and so give rise to a series of 2 to 40 antheridia (Fig. 32*A*). The protoplast of an antheridium may be metamorphosed into a single antherozoid, but usually it divides vertically or transversely to form two daughter protoplasts, each of which

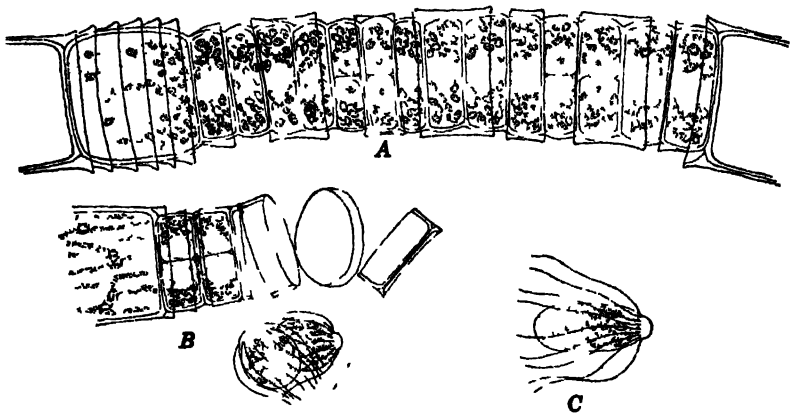


FIG. 32.—*Oedogonium crassum* (Hass.) Wittr. *A*, antheridium. *B*, liberation of antherozoids. *C*, free-swimming antherozoid. (× 185.)

becomes an antherozoid. Division of the antheridial nucleus is always in the transverse axis of the antheridium, but the two nuclei may come to lie one above the other before cytokinesis. Liberation of antherozoids is in the same manner as that of zoospores, and the antherozoids are likewise surrounded by a vesicle when first liberated (Fig. 32*B*). Except for the smaller size and fewer flagella, antherozoids of most species are like zoospores, but those of some species have flagella longer than the body of the antherozoid (Fig. 32*B*, *C*).

Oogonia of macrandrous species are formed by transverse division of an *oogonial mother cell* that may be terminal or intercalary in position. The distal daughter cell always matures into an oögonium (Fig. 33). Hence, oögonia always have one or more caps at the upper end. The lower daughter cell, the *suffultory cell*, may remain undivided, or it may function as an oogonial mother cell. In the former case the oogonia are solitary; in the latter they are in series of two or more. Each oogonium

[1] Gussewa, 1930; Ohashi, 1930. [2] Smith, G. M., 1933; Spessard, 1930

becomes more or less rounded and has a diameter greater than that of vegetative cells of the filament (As it approaches maturity, there is a formation of a small pore or a formation of a transverse crack in the oogonial wall The shape and position of this opening are quite characteristic for a species and are characters of diagnostic importance in separating species from one another The protoplast within an oogonium metamorphoses into a single egg The nucleus is centrally located within

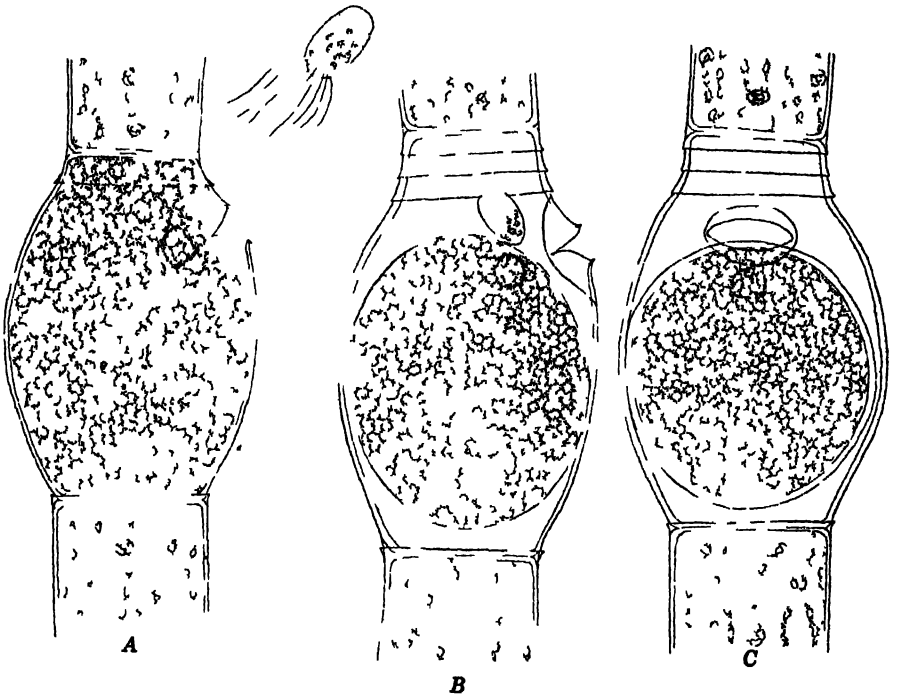


FIG 33 Oogonia of a macrandrous species of *Oedogonium O crassum* (Hass) Wittr *A* with the egg ready for fertilization *B* just after fertilization the antherozoid within the oogonium is probably a supernumerary one *C* zygote after the beginning of wall formation (×485)

a developing egg,[1] but shortly before fertilization it migrates to the egg periphery just within the opening in the oogonial wall Eggs ready for fertilization retract slightly from the oogonial wall and develop a hyaline receptive spot external to the nucleus)

The dwarf male filaments of nannandrous species are produced by the germination of special zoospores (*androspores*) that are produced within *androsporangia* Androsporangia (Fig 34*A*) are quite similar in appearance to the antheridia of macrandrous species If a nannandrous species is one with androsporangia and oogonia borne on the same filament, it is *gynandrosporous*, if the two are borne on separate filaments, the species is

[1] Klebahn, 1892, Ohashi, 1930

idioandrosporous. All nannandrous species are heterothallic. Androsporangia, similar to antheridia, are produced by unequal division of a mother cell. Only one androspore is formed within an androsporangium,[1] and, when it is first liberated, it is surrounded by a vesicle. After the vesicle disappears, the androspore swims freely in all directions until it comes in the vicinity of an oögonium or a developing oögonium. It then becomes affixed and germinates to form a dwarf male filament—the *nannandrium.* Androspores of certain species, as *O. concatenatum*

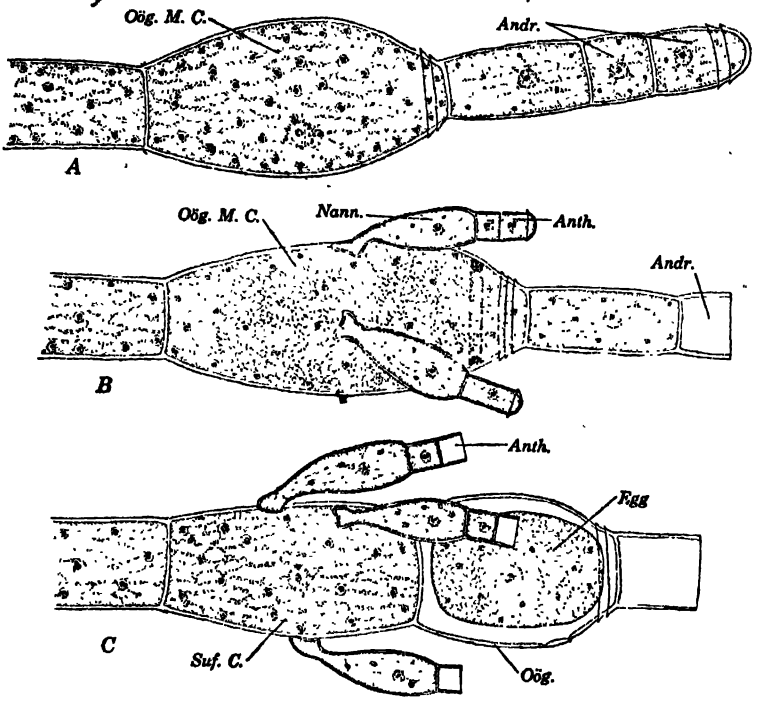


FIG. 34.—Sexual reproduction of a nannandrous species of *Oedogonium, O. concatenatum* (Hass.) Wittr. (*Andr.*, androsporangium; *Anth.*, antheridium; *Nann.*, nannandrium; *Oög.*, oögonium; *Oög.M.C.*, oögonial mother cell; *Suf. C.*, suffultory cell.) (× 325.)

(Hass.) Wittr., come to rest upon oögonial mother cells not yet divided into oögonium and suffultory cell (Fig. 34*B-C*). These species regularly bear their nannandria upon the suffultory cell. Other species usually liberate androspores after division of the oögonial mother cell, and their nannandria may be perched upon either oögonium or suffultory cell. One-celled germlings of nannandria are, except for their smaller size, quite like germlings developed from zoospores. One-celled germlings of most species function as antheridial mother cells and cut off one or more antheridia at their apices (Fig. 37*B*). The lower portion of the antheridial mother cell is never completely used up in the formation of antheridia and

[1] Hirn, 1900; Tiffany, 1930.

persists as a stipe supporting the antheridia. The protoplast of each antheridium divides to form two antherozoids, each with an apical crown of flagella.[1]

It is generally agreed that nannandrous species have been evolved from macrandrous ones. Some phycologists think that this has been brought about by a gradual reduction in size of male filaments of heterothallic macrandrous species. The occurrence of macrandrous species with somewhat smaller male filaments[2] and the precocious formation of antheridia by young filaments of heterothallic species[3] are held to be evidence for this. The similarity in structure and development of androsporangia and macrandrous antheridia indicates, however, that androsporangia have been evolved from antheridia. Androspores are, in a sense, macrandrous antherozoids that always develop parthenogenetically,[4] but which still retain sufficient of their gametic nature to swim to, and germinate upon, oögonia or cells related to them.

Oögonial development of nannandrous species is identical with that of macrandrous species.

Fertilization[5] in both nannandrous and macrandrous species is by the antherozoid swimming through the opening in the oögonial wall and entering the egg at the hyaline receptive spot (Fig. 33*A–B*). The male and female nuclei unite with each other in a resting condition and their fusion takes place soon after entrance of the antherozoid.[6] The zygote, which is somewhat retracted from the oögonial wall and of a different shape, begins to secrete a wall as soon as it is formed (Fig. 33*C*). Walls of mature zygotes are usually composed of three layers, but some species have a wall with two layers only. The layer outside the innermost may be smooth, but more often it is ornamented with pits, scrobiculations, reticulations, or costae. The color of the protoplast in a ripening zygote changes from green to a reddish brown, largely because of an accumulation of a reddish oil.

Some species have a regular development of unfertilized eggs into parthenospores; other species have a disintegration of eggs that are not fertilized. Parthenospores have a zygote-like wall, but they may be distinguished from zygotes by the fact that they completely fill the oögonial cavity and are of the same shape as the oögonium.[7]

The zygote is eventually liberated from the filament by a decay of the oögonial wall. It usually undergoes a further period of rest before germinating, and this may regularly last for a year or more.[7] During the ripening there is a reductional division of the zygote nucleus to form four

[1] Hirn, 1900; Tiffany, 1930.
[2] Hirn, 1900; West, 1912.
[3] Fritsch, 1902*A*.
[4] Schaffner, 1927.
[5] Hirn, 1900; Klebahn, 1892; Ohashi, 1930; Pringsheim, 1858.
[6] Gussewa, 1930; Klebahn, 1892; Ohashi, 1930.
[7] Mainx, 1931.

haploid nuclei.[1] Shortly before germination the protoplast becomes green and divides to form four daughter protoplasts, each of which becomes a zoospore.[2] The zoospores lie within a common vesicle when first liberated by a bursting of the zygote wall, but the vesicle soon disappears. The swarming and subsequent development of the zoospores into filaments are identical with those of zoospores produced by vegetative cells. In one macrandrous heterothallic species, it has been shown[3] that two of the four zoospores develop into male filaments and the other two into female filaments. Under certain cultural conditions, the zygote nucleus of this species divides equationally, and two diploid zoospores are formed when the zygote germinates. Both zoospores give rise to female filaments, but filaments which are double the size of haploid ones.

ORDER 8. ZYGNEMATALES

The Zygnematales (Conjugales) differ from all other Chlorophyceae in their lack of flagellated reproductive cells and their sexual reproduction by amoeboid gametes. The organization of the protoplast is also distinctive

The order includes some 38 genera and 2,750 species, all fresh-water in habit.

The cells may be solitary or united end to end in unbranched filaments Cell walls of Zygnematales are generally composed of two concentric layers: a cellulose layer next to the protoplast and an outer layer of pectic material. Filamentous Zygnematales are usually slippery to the touch because of the mucilaginous sheath of pectose The chloroplasts are of three general types: peripheral spirally twisted bands extending the length of the cell; an axial plate extending the length of the cell; or two stellate chloroplasts axial to each other. There are many modifications of the last-named type among the Desmidiaceae, and many members of this family have "stellate" chloroplasts from which the central mass has entirely disappeared.

None of the Zygnematales forms asexual reproductive bodies. All genera reproduce sexually by a fusion of amoeboid gametes. Gametes are formed singly within a cell, and in most genera all of the protoplast is used in production of a gamete. Gametic union may be through a tubular connection established between two cells, or the gametes may escape from their enclosing walls at the time they fuse with each other. The zygote develops a thick wall and enters upon a period of rest before it germinates. The fact that all cytologically investigated species[4] have a reduction

[1] Gussewa, 1930; Mainx, 1931

[2] Gussewa, 1930; Jurányi, 1873; Mainx, 1931; Pringsheim, 1858.

[3] Mainx, 1931

[4] Kauffmann, 1914; Kurssanow, 1911; Potthoff, 1927; Trondle, 1911.

division of the zygote nucleus seems to justify the assumption that vegetative cells of all Zygnematales are haploid. Depending upon the genus, a germinating zygote gives rise to one, two, or four new plants.

Many phycologists consider the Zygnematales a class coördinate with the Chlorophyceae or a subclass of the Chlorophyceae. Whether they are to be considered a group greater in magnitude than an order depends upon their relationship to other Chlorophyceae. If they represent a phylogenetic series evolved directly from the Volvocales (but with all intermediates lost), they may possibly merit recognition as a subclass. The occasional occurrence of amoeboid instead of flagellated gametes in *Chlamydomonas*[1] and the presence of various types of chloroplast in this genus suggest the possibility of a derivation of the Zygnematales from one-celled motile ancestors. On the other hand, cells of Zygnematales have the same ability to divide vegetatively as is found in the tetrasporine species of Chlorophyceae. Primitive and advanced tetrasporine Chlorophyceae also have the capacity to form amoeboid instead of flagellated reproductive cells.[2] There is, therefore, an equal possibility that the Zygnematales are an offshoot from the tetrasporine line that may have arisen at an early or a relatively late stage in evolution of the tetrasporine series.

Most phycologists divide the Zygnematales into two families: one containing the truly filamentous genera; the other the unicellular genera and their relatives (collectively known as the *desmids*). Modern students recognize two distinct series among the desmids and give each the rank of a family.

FAMILY 1. ZYGNEMATACEAE

The Zygnemataceae have cylindrical cells that are permanently united in unbranched filaments. The cells have unsegmented walls that are without pores. The protoplast may contain one or more peripheral spiral ribbon-shaped chloroplasts, a single axial laminate chloroplast, or two axial stellate chloroplasts. At the time of sexual reproduction there is an establishment of a tubular connection between two cells and never an escape of the amoeboid gametes from the surrounding walls.

There are about 10 genera and 380 species, all fresh-water in habit.

The well-known *Spirogyra* is a member of the family. *Zygnema*, with some 65 species, is also widely distributed. It has cells with two stellate chloroplasts, but one may not be certain that any vegetative filament with such cells is *Zygnema*, because cells of certain other Zygnemataceae also have two stellate chloroplasts. The cells of *Zygnema* are cylindrical and usually with a length not more than twice the breadth. Lateral walls of filaments of *Zygnema* rarely have a thick pectose layer,[3] and there

[1] Pascher, 1918. [2] Pascher, 1915. [3] Tiffany, 1924.

is never the refolding (replication) of the transverse wall that is found in certain species of *Spirogyra*. Most filaments have all cells alike, but occasionally[1] certain cells of a filament develop rhizoid-like outgrowths (*haptera*).

Protoplasts of *Zygnema* contain two stellate chloroplasts that lie axial to each other in the longitudinal axis of a cell (Fig. 35*A*). The chloroplasts have numerous delicate to massive strands extending to the plasma

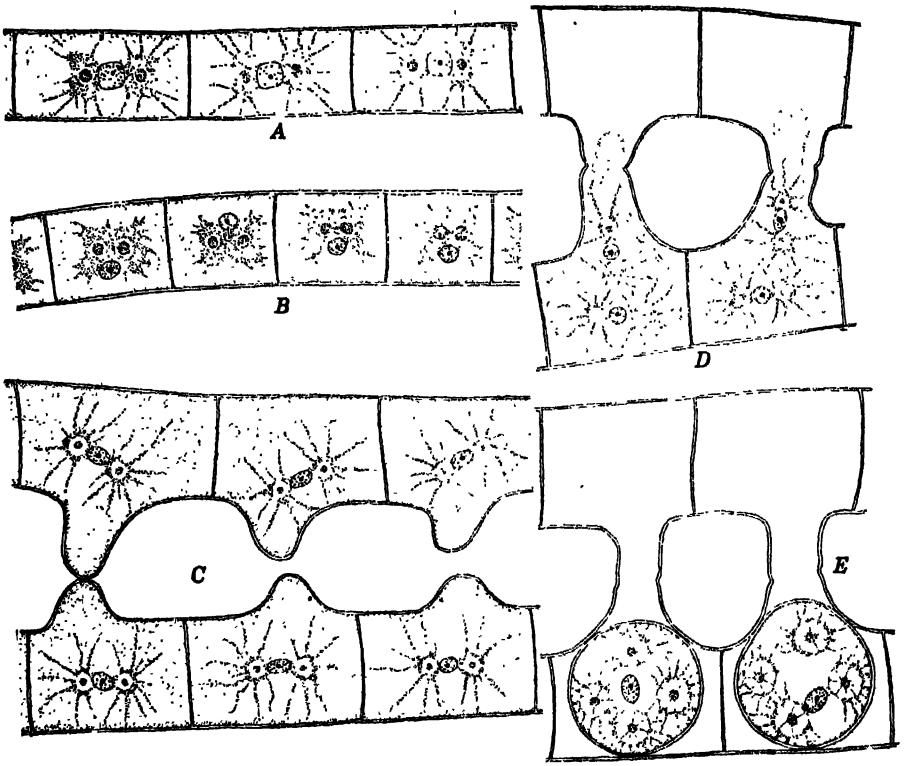


FIG. 35.—*Zygnema* spp. *A*, mature vegetative cells. *B*, recently divided cells. *C–E*, stages in sexual reproduction. (× 430.)

membrane. A chloroplast has a single large pyrenoid at its center. The cells are uninucleate, with the nucleus embedded in a broad strand of cytoplasm connecting the two chloroplasts. Division of the nucleus is mitotic.[2] It usually begins early in the evening and is often completed shortly after midnight.

Cell division follows very shortly after nuclear division; it is transverse and due to an annular furrowing of the plasma membrane midway between the ends of a cell. In cell division each daughter cell receives

[1] Borge, 1894; Iyengar, 1923.

[2] Escoyez, 1907; Merriam, 1906; van Wisselingh, 1913.

one of the chloroplasts of the parent cell. The nucleus of a recently divided daughter cell lies lateral to the chloroplast and midway between the poles of the cell (Fig. 35*B*). Later on there is a division of the chloroplast, accompanied by a division of the pyrenoid and a migration of the nucleus to a position midway between the two daughter chloroplasts.[1]

Cell division increases the number of cells in a filament but does not result in a direct increase in number of filaments. *Zygnema* may reproduce vegetatively by an accidental severing of filaments, and the rapid increase in number of them when the alga is growing in quiet water shows that this is an efficient method of reproduction. In very rare cases there is a vegetative multiplication by disjunction into individual cells or into fragments with a few cells each. One terrestrial species has been reported[2] as forming thick-walled resting cells. Such thick-walled cells of Zygnemataceae are usually called "akinetes," but they are not strictly comparable to the akinetes of Ulotrichales and other Chlorophyceae because there is not a true spore wall fused with the wall of the vegetative cell.

Cells of *Zygnema* may also have a rounding up of the protoplast and a secretion of a thick wall about the retracted protoplast. For any given species, the structure and ornamentation of the special walls surrounding these bodies are identical with wall structure of zygotes. It is therefore much more fitting to term them *parthenospores* or *azygotes* (azygospores) than to call them aplanospores. The gametic nature of parthenospores is clearly evident in conjugating filaments when they result from the failure of gametes to unite with one another. Practically all collections of fruiting *Zygnema* contain one or more parthenospores of this nature. A few species regularly form parthenospores in greater number than zygotes, or form parthenospores only.

There is a marked seasonal periodicity of sexual reproduction and each species usually fruits at a definite time of the year. Most species fruit in the spring. The time of fruiting of *Spirogyra* has been shown[3] to be directly correlated with the ratio between the surface and volume of the cell, and the same is thought to be true for *Zygnema*. Vegetative cells of *Zygnema* function directly as gametangia, and each cell produces a single nonflagellate gamete. All cells of a filament are potentially capable of producing gametes, and at the time of fruiting there is a simultaneous production of gametes by all or almost all cells of a filament. At the time of gametic union the gametangia are connected in pairs by a conjugation tube. The tubular connection may be established between cells of different filaments (*scalariform conjugation*) or between adjoining cells of the same filament (*lateral conjugation*). Conjugation of *Zygnema* is usually scalariform.

[1] Escoyez, 1907; Merriam, 1906. [2] De Puymaly, 1922A. [3] Transeau, 1916.

Scalariform conjugation begins with an approximation of two filaments so that they lie side by side throughout their entire length. Small dome-shaped protuberances next grow toward each other from opposed pairs of cells, and each protuberance elongates until it becomes a short cylindrical outgrowth (Fig. 35*C*). The cylindrical outgrowths from opposite cells come in contact; the wall of each is digested at the point of mutual contact; and with the establishment of the opening the two outgrowths become a conjugation tube. In some species both gametes become amoeboid and migrate into the conjugation tube where they fuse with each other to form the zygote In other species one of the gametes

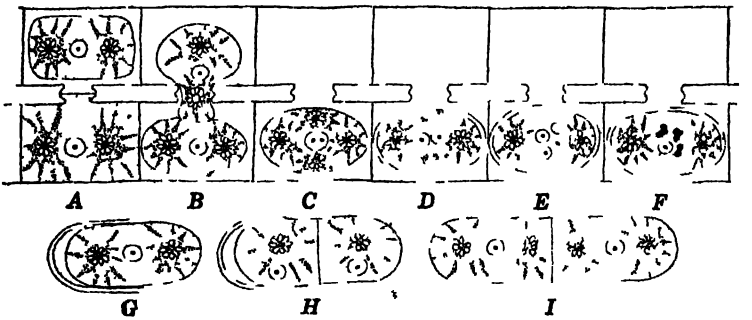


FIG 36 —Diagram of zygote formation and germination in *Zygnema*

(the male) is actively amoeboid, and the other (the female) is passive Gametic union in such species takes place in the female gametangium (Fig. 35*D*). Sexual differentiation in these species may be recognized at a relatively early stage of conjugation because of the earlier shrinkage of the male protoplast and its rotation so that the two chloroplasts stand perpendicular to the developing conjugation tube

Union of the two gamete nuclei in a zygote may take place at once or may be delayed for a time (Fig 35*E*) The four chloroplasts persist for a time, but there is an eventual disintegration of the two lying in the short axis of the zygote,[1] and it is very probable that the degenerating chloroplasts were contributed by the male gamete (Fig 36*B D*). Development of a wall about a zygote begins quite early, but it does not become fully developed for several weeks. A mature wall consists of a thin inner layer of cellulose, a thin outer layer of cellulose or pectose, and a thick median layer of cellulose that may be more or less chitinized.[2] The coloration and ornamentation characteristic of a zygote of a particular species are usually developed in the median wall layer. The zygotes are eventually liberated by a decay of the gametangial or the conjugation tube walls. They rarely germinate as soon as they appear to be mature; and it is very probable that in the majority of species there is no germination until the spring following their formation.

[1] Kurssanow, 1911. [2] Tiffany, 1924.

Prior to germination there is a reduction division of the zygote nucleus[1] (Fig. 36). Three of the resultant haploid nuclei degenerate; the fourth remains unchanged until the zygote germinates (Fig. 36*D–F*). At the time of germination there is a rupture of the two outermost zygote wall layers. The protoplast, still surrounded by the innermost wall layer, may escape from the outer layers (Fig. 36*G–I*) or only partially escape from them.[2] In either case it divides transversely, and the two daughter cells divide and redivide to form a filament.

FAMILY 2. MESOTAENIACEAE

The Mesotaeniaceae, the "saccoderm" desmids, have uninucleate cells of various shape, and they may be solitary or united in simple filaments. The cell walls are without pores, and dividing cells do not

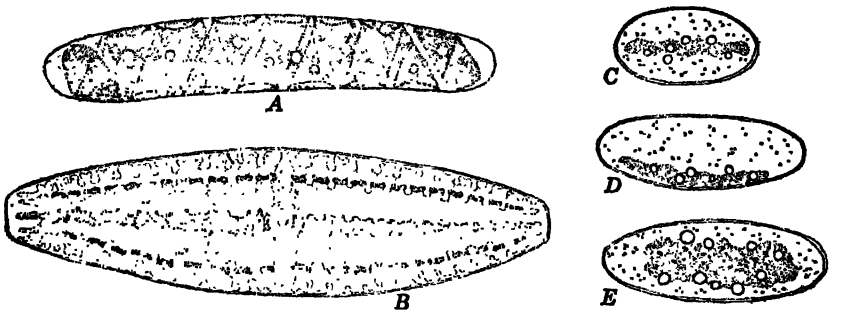


FIG. 37.—Vegetative cells of various Mesotaeniaceae. *A*, *Spirotaenia condensata* Bréb. *B*, *Netrium digitus* (Ehr.) Itz. and Rothe. *C–E*, *Mesotaenium Greyii* var. *breve* W. West. (*A–B*, × 400; *C–E*, × 485.)

have the regeneration of a new "half cell" that is found in "placoderm" desmids. Conjugation is generally by means of a definite conjugation tube.

The family includes 7 genera and about 75 species. All species are fresh-water in habit, and most of them are restricted to soft waters.

Cell walls of Mesotaeniaceae (Fig. 37) are unsegmented, without pores, and never impregnated with iron compounds.[3] Most genera have a wall composed of two concentric layers, but some have one with three layers. The innermost layer consists almost wholly of cellulose and the outermost almost wholly of pectose. The gelatinous pectic layer may be quite broad, and in some cases sheaths of cells are confluent with one another to produce an amorphous mucilaginous mass containing many cells.

Chloroplasts of Mesotaeniaceae are of the same three types that are found in the Zygnemataceae.[4] Cells of the three types have their nuclei localized as in the corresponding types among the Zygnemataceae.

[1] Kurssanow, 1911. [2] DeBary, 1858; Kurssanow, 1911.
[3] Höfler, 1926; Lütkemüller, 1902. [4] Carter, Nellie, 1919*A*, 1920*A*.

The meager accounts of cell division among Mesotaeniaceae[1] indicate that the method of division is identical with that of Zygnemataceae. Increase in length seems to take place throughout the entire length of the daughter cells and not, as in Desmidiaceae, by the formation of a new semicell. Cell division is usually followed by an immediate separation of the daughter cells as a result of disintegration of the middle lamella between them. In at least two of the genera the cells usually remain united end to end for several cell generations, but such filaments readily dissociate into single cells when disturbed.

Conjugation has been recorded for all genera. In some genera it is of frequent occurrence, in others it is infrequent. The process is initiated

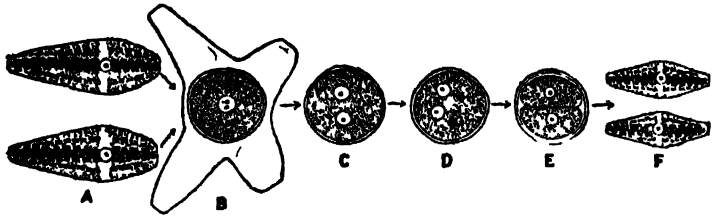


FIG. 38.—Diagram of the formation and germination of the zygote of *Netrium digitus* (Ehr.) Itz. and Rothe. (*Diagram based upon Potthoff*, 1928.)

by two cells becoming enveloped by a common gelatinous sheath. The pair of cells may lie parallel to, or at right angles with, each other. Conjugation is usually between fully mature cells, but in *Netrium*[2] it takes place between recently divided ones. Most species establish a conjugation tube similar to that of Zygnemataceae, and those with a conjugation tube have the zygote formed in the tube.

Zygotes of Mesotaeniaceae have a thick wall and usually one composed of three layers. However, these zygotes do not have the elaborate sculpturing and spinescence so often found in those of Desmidiaceae.

Two genera have been shown[3] to have a reduction division of the nucleus in a ripening zygote and a formation of four functional nuclei. One genus[2] has the fusion nucleus dividing reductionally to form two functional and two nonfunctional nuclei (Fig. 38). The nuclear divisions are followed, respectively, by a division of the protoplast into four or into two daughter protoplasts. This may take place before or after rupture of the outer zygote wall layers.

FAMILY 3. DESMIDIACEAE

The Desmidiaceae, the "placoderm" desmids, have cells which may be solitary, united end to end in filamentous colonies, or united in amorphous

[1] DeBary, 1858; Kauffmann, 1914; West, 1915. [2] Potthoff, 1928.
[3] Kauffmann, 1914; Potthoff, 1928.

colonies. In all but two genera the cells have an evident median constriction (*sinus*), dividing them into two distinct halves (*semicells*) joined together by a connecting zone (the *isthmus*). Cells of various genera are diverse in form, but all of them have walls that are transversely segmented and with vertical pores. Conjugating cells usually have their protoplasts escaping from the surrounding walls as they unite to form a zygote.

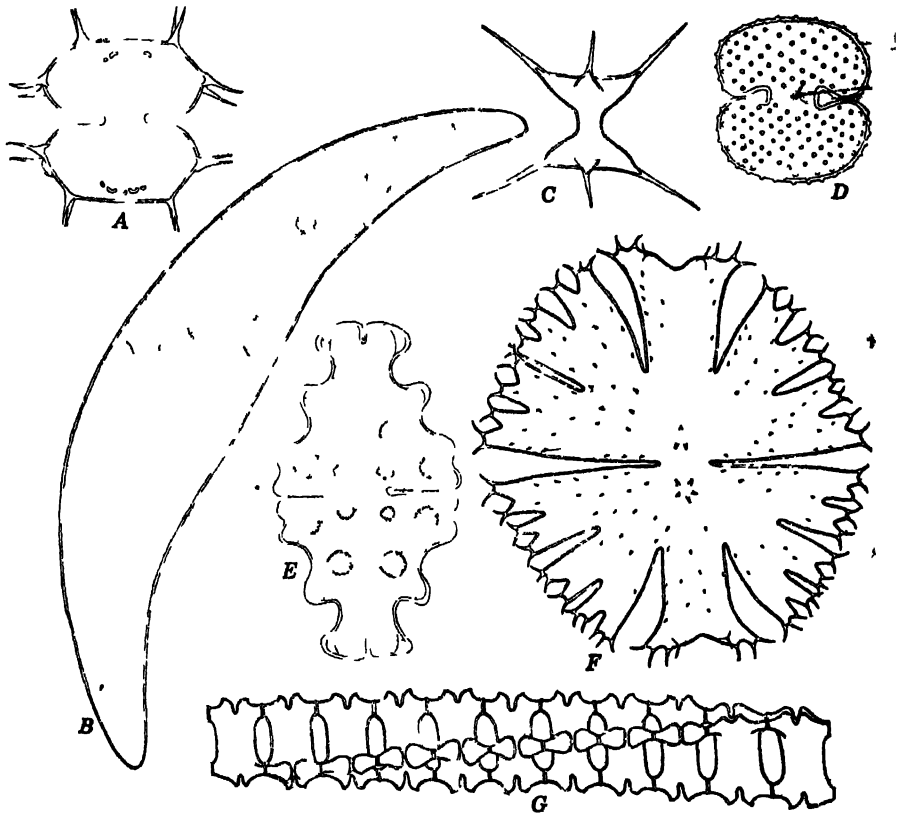


FIG. 39 Vegetative cells of various Desmidiaceae. *A*, *Xanthidium antilopaeum* var. *polymazum* Nordst. *B* *Closterium moniliforme* (Bory) Ehr. *C*, *Staurastrum curvatum* W. West. *D*, *Cosmarium reniforme* (Ralfs) Arch. *E*, *Euastrum affine* Ralfs. *F*, *Micrasterias apiculata* (Ehr.) Menegh. *G*, *Desmidium Aptogonum* Brēb. (× 400.)

There are 21 genera and some 2,300 species, all fresh-water. Desmidiaceae are found sparingly intermingled with free-floating algae everywhere, but collections rich in species and in number of individuals are usually made only when the waters have a pH of 5 to 6. Most genera are immediately recognizable because their cells are transversely constricted into two symmetrical halves. Generic distinctions are based entirely upon shape and structure of vegetative cells (Fig. 39). Specific

distinctions are based in part upon cell shape and in part upon ornamentation of the cell wall. In many genera the cell must be examined in both front and vertical view before the species can be determined with accuracy.

Walls of all Desmidiaceae have three concentric layers. The innermost layer is thin and composed entirely of cellulose; the median layer is somewhat thicker and has a substratum of cellulose that is impregnated with pectic compounds; the outer layer is a gelatinous sheath of pectose that may be narrow or very broad. The two inner layers are perforated by vertical pores[1] that are usually arranged in a definite pattern. Pores may be present on all parts of a wall except the isthmus, or they may be localized in definite parts of each semicell. The pores are filled with a pectic material that is often of a tougher consistency than, and extends into, the watery sheath of pectic material. Sometimes the gelatinous material extending through the pores is evident in living cells, but more often it is only evident when the walls have been stained with special reagents.[1] Many Desmidiaceae have brown cell walls because of an impregnation with iron salts. The salts are localized chiefly in the median layer, and they may be uniformly distributed over the entire layer or restricted to certain portions of it.[2] Many Desmidiaceae move over the bottom and toward the side when they are placed in an aquarium Movement is in a series of jerks, and it has been shown[3] to be intimately connected with a localized secretion of gelatinous material through pores at one end of the cell.

In the vast majority of Desmidiaceae there is at least one chloroplast in each semicell.[4] A few species with very small cells have a single chloroplast extending the entire length of the cell. Semicells with one chloroplast have it axial in position; those with two chloroplasts usually have them axial and lateral to each other. Species with four or more chloroplasts in each semicell have them parietal in position. There is great diversity in the profile of chloroplasts from species to species, and in many cases the outline is further complicated by plate-like outgrowths. In some species there is little variation in form of the chloroplast from cell to cell; in other species there is so marked a tendency to vary that the majority of individuals do not conform to any given type. Small chloroplasts regularly have but one or two pyrenoids, which are more or less median in position; large massive chloroplasts usually have numerous indiscriminately scattered pyrenoids

Certain genera with elongate cells have a spherical vacuole at each end of the cell. The vacuoles contain one or more vibrating granules.

[1] Lutkemuller, 1902. [2] Hofler, 1926.
[3] Klebs, 1885; Kol, 1927; Schröder, 1902
[4] Carter, Nellie, 1919*A*, 1919*B*, 1920, 1920*A*.

The granules have been shown[1] to be crystals of gypsum, and it has been held[2] that they function as statoliths.

The nucleus always lies at the isthmus and is often connected with string-like extensions of the chloroplasts. This connection is quite firm and persists even when the nuclei have been laterally displaced by centrifuging.[3] In the few cases where nuclei have been studied cytologically,[4] they have been shown to have a conspicuous nucleolus and a more or less well-defined chromatin-linin network.

There have been no critical investigations of cell division (Fig. 40) among genera whose cells have a conspicuous isthmus. It is well known that Desmidiaceae with this type of cell have division of the nucleus followed by an elongation of the isthmus. There is next a transverse

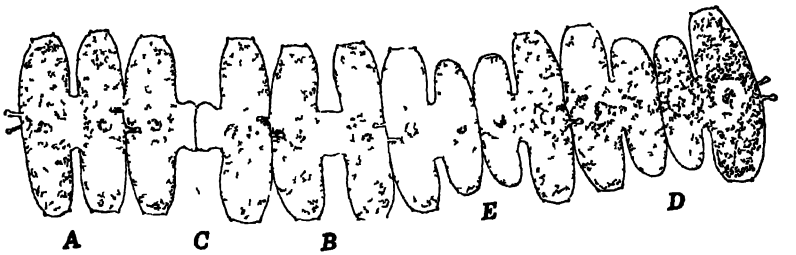


FIG. 40 — Cell division in *Sphaerozosma Aubertianum* var. *Archeri* (Gutw.) W. and G. S. West. *A*, undivided cell. *B–E*, successive stages in division. (×730.)

division at the elongated isthmus, after which the portion of the isthmus attached to each old semicell enlarges to form a new semicell. Division of the chloroplast or chloroplasts in each of the original semicells takes place during development of the new semicells. New pyrenoids may be formed by a division of those present in a chloroplast[5] or may be formed *de novo*.[3] Occasionally there is a complete or incomplete failure of cell division as the isthmus starts to elongate. Continued enlargement of the isthmus results in a monstrous cell in which an abnormally shaped structure is intercalated between two semicells.

Aplanospores have been recorded for a few species, but most of these so-called aplanospores are parthenospores. Possibly the spore-like bodies formed in cells of one genus[6] are true aplanospores since their shape is not the same as that of the zygotes.

Zygotes (Fig. 41) have been described for many species of Desmidiaceae, but they are of infrequent occurrence and one is rarely fortunate enough to collect material rich in fruiting specimens. Conjugation usually takes place between fully mature cells, but sometimes it is between recently divided ones. In some cases the juvenile conjugating

[1] Fischer, 1884. [2] Steinecke, 1926. [3] Carter, Nellie, 1919*A*.
[4] Acton, 1916; Klebahn, 1891; Lutman, 1911; Potthoff, 1928.
[5] Acton, 1916. [6] Roy and Bissett, 1893, 1894.

cells are sister cells. Conjugation of solitary free-floating species takes place between two cells that lie within a common gelatinous envelope. All but four or five species form a single zygote within the common gelatinous envelope. The four or five exceptional species form twin zygotes, and in certain cases this has been shown to be due to conjugation

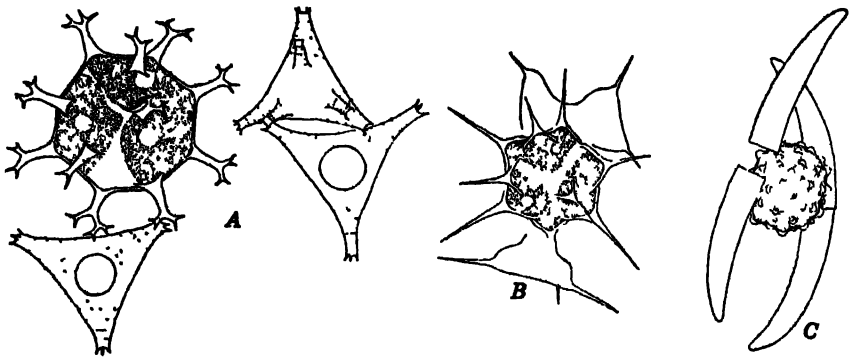


FIG. 41.—Zygotes of Desmidiaceae *A*, *Staurastrum fucigerum* Bréb. *B*, *Arthrodesmus incus* var. *extensus* Anderss. *C*, *Closterium calosporum* Wittr. (*A*, *C*, × 300; *B*, × 600.)

in pairs between four young daughter cells lying within a common envelope. Almost all unicellular species have the two cells within an envelope breaking open at the isthmus and both protoplasts moving out from the cell walls and meeting midway between the two. A few unicellular[1] and filamentous[2] species develop a conjugation tube. Species with a conjugation tube generally have the zygote formed in the tube.

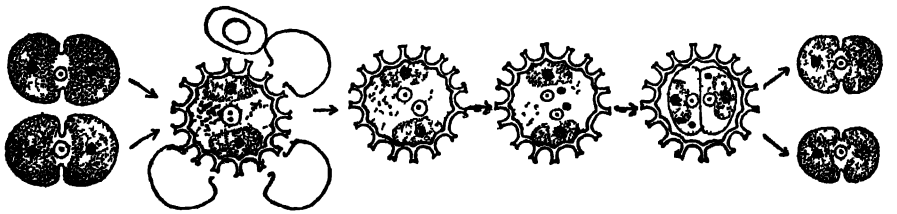


FIG. 42.—Diagram of the formation and germination of the zygote of *Cosmarium*. (*Diagram based upon Klebahn*, 1891.)

Zygotes of Desmidiaceae have a wall composed of three layers. The outermost layer often develops spines or warts distinctive of the species.

Gametic union (Fig. 42) is followed by a fusion of the two nuclei. Species with a single chloroplast contributed by each gamete have one chloroplast disintegrating as the zygote matures;[3] those with two chloroplasts from each gamete have two chloroplasts disintegrating.[4] Three genera have been shown[5] to have two successive divisions of the fusion

[1] Scherffel, 1928. [2] Carter, Nellie, 1923. [3] Potthoff, 1927
[4] Klebahn, 1891. [5] Klebahn, 1891; Potthoff, 1927.

nucleus, followed by a partial disintegration of two nuclei formed by the second division. Division of the zygote nucleus has been shown[1] to be meiotic in one of the genera, and the same is probably true of the other two. In all three genera the protoplast of a germinating zygote divides into two daughter protoplasts, both of which contain a single chloroplast, a functional nucleus, and a degenerating nucleus. Each of the two protoplasts develops into a vegetative cell after liberation by a rupture of the zygote wall. A fourth genus has been described[2] as having a formation of four nuclei within a ripening zygote and a production of one, two, three, or four cells by the germinating zygote.

ORDER 9. CHLOROCOCCALES

Cells of Chlorococcales may be solitary or colonial and with either a definite or an indefinite number of cells in a nonfilamentous colony. Cells may be uninucleate or multinucleate, but in neither case do they divide vegetatively. Asexual reproduction is by means of zoospores or autospores. Sexual reproduction, when present, is by a fusion of biflagellate gametes.

The order includes about 90 genera and 700 species. Almost all of the species are fresh-water, and many of them are found only in the plankton of ponds and lakes.

The Chlorococcales lie in the third of the evolutionary lines from the motile unicellular condition (page 25). In this evolutionary series there has been an obliteration of all vegetative cell divisions, and there is no division of the protoplast except immediately before the formation of zoospores, gametes, or other reproductive bodies. Some members of the order are unicellular. Others form colonies as a result of apposition of zoospores or autospores liberated from a parent cell or as a result of the cells remaining within a common matrix produced by a gelatinization of the parent-cell wall. Loss of the ability to divide vegetatively has not always been accompanied by an obliteration of nuclear divisions, and there are multinucleate Chlorococcales with a limited or an indefinite number of nuclei. In some Chlorococcales with an indefinite increase in number of nuclei, there is also a tendency toward an indefinite increase in length and size of the cell. Evolution along this line produced the Siphonales, and there are certain borderline green algae, as *Protosiphon*, that some phycologists place among the Chlorococcales and others among the Siphonales.

Some of the Chlorococcales reproduce by means of zoospores. They may be formed by a repeated bipartition of the protoplast, by a simultaneous cleavage, or by a progressive cleavage. The zoospores are usually biflagellate and ovoid to pyriform. Swarming zoospores may

[1] Potthoff, 1927. [2] Turner, 1922.

swim away from one another and develop into solitary vegetative cells, or the mass of zoospores may remain within a common envelope and become organized into a colony with a definite number of cells. Many genera reproduce only by means of aplanospores with a shape similar to that of the vegetative cell. Such *autospores* may separate from one another when liberated from the parent-cell wall, or they may remain within the gelatinized parent-cell wall. Autospores liberated from a parent-cell wall may also remain apposed to one another and produce an autocolony with the cells arranged in a specific manner.

Zoosporic genera may also reproduce by means of flagellated gametes. Fusing gametes of most genera are equal in size, but a few genera are anisogamous. The zygotes of certain genera develop directly into vegetative cells. In one of them, *Chlorochytrium*, the nucleus has been shown to be diploid. Such a condition is quite different from that of other Chlorococcales where the zygote is a resting cell and where the vegetative functions, especially photosynthesis, center in the haploid phase of the life cycle.

The Chlorococcales are variously divided into seven to nine families. Certain of them (Hydrodictyaceae, Scenedesmaceae) are natural; others (as the Oöcystaceae and Chlorococcaceae) are more or less artificial, and the various genera of these families have but little in common aside from the method of reproduction.

FAMILY 1. CHLOROCOCCACEAE

The Chlorococcaceae include the zoosporic unicellular genera in which the cells are more or less globose and apparently haploid. The cells are usually uninucleate. Chloroplasts are of various shapes from genus to genus. Asexual reproduction is by means of zoospores (sometimes also aplanospores) that separate from one another after liberation. Sexual reproduction is by the fusion of biflagellate gametes.

The family includes about 10 genera and 40 species, all fresh-water.

Chlorococcum, with several species, is a subaerial alga that sometimes grows in abundance on damp soil or on brickwork. The cells may be solitary, or they may be gregarious and either in a pulverent mass or embedded in a gelatinous matrix. One of the features distinguishing this genus from most other unicellular green algae is the striking variation in size of vegetative cells of any given species (Fig. 43*A–C*). Young cells are thin walled and spherical or somewhat compressed. Old cells have thick walls; walls that are often irregular in outline because of local button-like thickenings. Thickened portions of walls are often distinctly stratified. Chloroplasts of young cells are parietal massive cups, completely filling the cell cavity except for a small hyaline region at one side. They contain one pyrenoid. Old cells have a diffuse

chloroplast that generally contains many starch grains and sometimes droplets of oil. The cells are uninucleate until shortly before reproduction.[1]

There is never an increase in the number of cells by vegetative division, and all formation of new cells is due to a germination of zoospores or aplanaspores. Reproduction by means of zoospores may take place at almost any stage in the enlargement of a cell.[2] Small cells usually form 8 to 16 zoospores; large cells produce many zoospores (Fig. 43*D–E*). The cells are multinucleate at the time of reproduction, and there is a progressive cleavage into uninucleate protoplasts by an inward furrowing of the plasma membrane.[3] Each uninucleate protoplast is metamorphosed into a zoospore, and the zoospores are liberated through an aperture in the parent-cell wall. The zoospores (Fig. 43*F*) are ellipsoidal

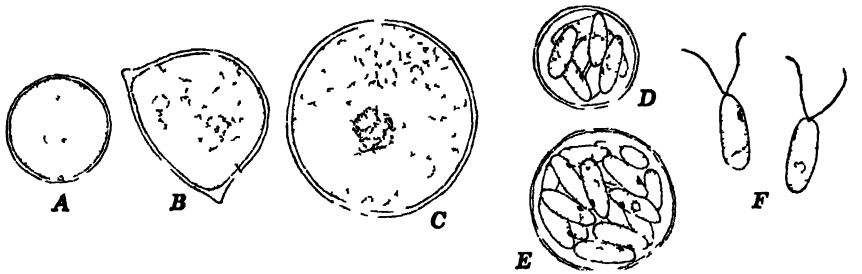


FIG 43 — *Chlorococcum humicola* (Nag.) Rab. *A–C*, vegetative cells *D–E*, cells containing zoospores *F*, zoospores (× 800)

and biflagellate, and with an eyespot and a cup-shaped chloroplast. Uninucleate protoplasts formed by progressive cleavage may develop into aplanospores instead of into zoospores. The parent-cell wall may burst as the aplanospores begin to enlarge into vegetative cells, and most of the enlargement takes place after the aplanospores are liberated,[3] or the aplanospores may remain within the old parent-cell wall until the latter gelatinizes. This results in a *Palmella* stage. Cells of *Palmella* stages divide to form two or four naked daughter cells that become flagellated and function as gametes.[4]

Sexual reproduction is also by means of biflagellate gametes formed by division of protoplasts of ordinary vegetative cells.[5] These gametes are formed in the same manner as zoospores.

Trebouxia is found both in the thalli of lichens and as a free-living aerial alga. Many species have been described, but those found in a majority of lichens cannot be distinguished morphologically from *T. Cladoniae* (Chod.) G. M. Smith. *Trebouxia* is not the only unicellular green alga in lichens,[6] but it is the one most often encountered. The

[1] Bold, 1931; Bristol, 1919. [2] Artari, 1892; Bristol, 1919. [3] Bold, 1931.
[4] Bristol, 1919. [5] De Puymaly, 1924. [6] Chodat, 1913.

cells are usually spherical, but they may be ovoid or pyriform. The cell walls are always thin, and they never have the irregular thickenings that are found in walls of *Chlorococcum*. *Trebouxia* differs from the great majority of genera in the family in having a massive centrally located chloroplast that extends nearly to the plasma membrane (Fig. 44*A–C*). The outline of the chloroplast is usually irregular and lobed. There is a single pyrenoid at the center of a chloroplast. The single nucleus of a cell lies at one side of the chloroplast and just within the plasma membrane

There is never a multiplication by vegetative cell division. Reproduction by means of zoospores has been repeatedly observed[1] when the

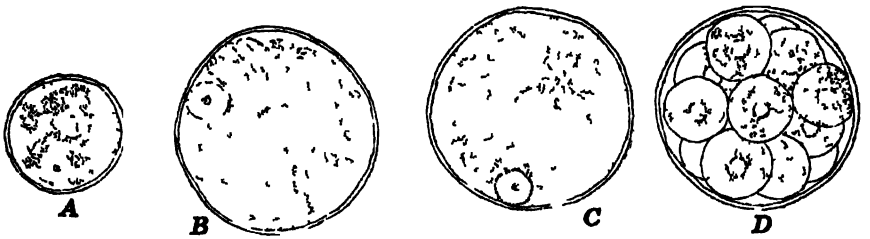


FIG 44.—*Trebouxia Cladoniae* (Chod.) G. M. Smith. *A–C*, vegetative cells. *D*, a cell containing aplanospores. (× 1950.)

alga is growing in a liquid medium. It is very probable that zoospores are also formed under natural conditions during rainy periods. The zoospores are subspherical to subellipsoidal, are biflagellate, and have a chloroplast at the posterior end. Liberation of zoospores is through an opening at one side of the parent-cell wall, and they may escape singly through the opening or be extruded in a mass.[2] In most cases asexual reproduction is by means of autospores (Fig. 44*D*) instead of zoospores. Eight to a hundred or more of them are produced within a cell, and they may be liberated from the parent-cell wall soon after their formation or they may be retained within the wall until they have grown to a size equal to that of adult vegetative cells.

Sexual reproduction is by the fusion of biflagellate gametes that may be of equal or unequal size.[2]

FAMILY 2. ENDOSPHAERACEAE

The Endosphaeraceae are unicellular and generally with large irregularly shaped cells. Most of them grow endophytically within tissues of marine algae, mosses, or angiosperms. Their chloroplasts may be parietal or central in position and with one or many pyrenoids.

[1] Chodat, 1913; Famintzin, 1914; Famintzin and Boranetzky, 1867; Jaag, 1929.
[2] Jaag, 1929.

One genus is strictly parasitic and is without chloroplasts or pyrenoids. Reproduction is by means of biflagellate zooids.

The family includes about 4 genera and 20 species.

In some species there is always a fusion of the zooids in pairs;[1] in other species there is never a fusion;[2] in still other species there may or may not be a fusion to form a zygote.[3] Although our knowledge of these algae is still too fragmentary to warrant a definite statement, it is not impossible that all zooids are gametic in nature. If this be true, the cases where the swarmers germinate directly into vegetative cells must be interpreted as parthenogenesis rather than as an asexual reproduction by means of zoospores. There is also the possibility that all species with gametic union are similar to *Chlorochytrium Lemnae* Cohn and have diploid vegetative cells.

Chlorochytrium, with about 10 species, grows endophytically in other plants. Fresh-water species grow within tissues of mosses and angio-

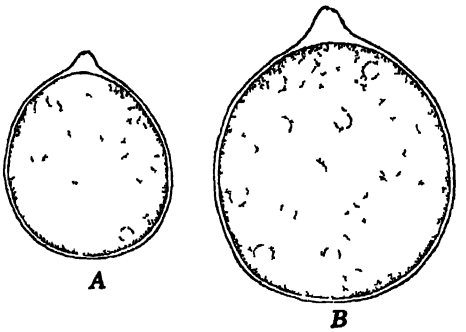


FIG. 45.—*Chlorochytrium inclusum* Kjellm. • (× 440)

sperms. Marine species grow within tissues of various membranous or expanded Rhodophyceae. The cells of *Chlorochytrium* are irregularly globose or ellipsoidal (Fig. 45). Walls of mature cells may be thick and stratified, or relatively thin and homogeneous. Either type of wall may have localized lamellated thickenings. Chloroplasts of young cells are parietal and cup-shaped,[4] but, as the cell increases in size, the chloroplasts come to fill the entire cell. A chloroplast may have a smooth surface, or it may have[5] numerous radial projections. Young cells of *C. Lemnae* Cohn are uninucleate. As the cell grows in size, the nucleus increases in volume but does not divide.[6] Reproduction is preceded by a repeated series of simultaneous nuclear divisions in which the first is reductional.[6] There is a transverse cytokinesis after the first nuclear division and a further bipartition after each mitosis. Nuclear

[1] Gardner, 1917; Klebs, 1881. [2] Bristol, 1917; Reichardt, 1927.
[3] Griggs, 1912; Klebs, 1881. [4] Cohn, 1872. [5] Bristol, 1920.
[6] Kurssanow and Schemakhanova, 1927.

division and cytokinesis may continue until 256 uninucleate protoplasts are formed. These uninucleate protoplasts are then metamorphosed into biflagellate gametes that escape from the old parent-cell wall. The gametes fuse in pairs[1] to form a quadriflagellate zygote that swarms for a short time and then settles down upon the host, loses its flagella, and secretes a wall. Fusion of the two gamete nuclei may be completed before secretion of the zygote wall.[2] The side of the zygote next to the host soon sends out a tubular protrusion that grows between the host cells and enlarges at the distal end.[3] The entire protoplast of the zygote moves into the enlarged end of the protrusion and there develops into a large vegetative cell.

FAMILY 3. CHARACIACEAE

The Characiaceae have sessile elongate cells that may be solitary or joined to one another in radiate colonies. The cells are usually multinucleate, although sometimes they are uninucleate. Most genera have a single parietal laminate chloroplast containing one or more pyrenoids. One genus has cells without chloroplasts. Asexual reproduction is usually by means of zoospores, but it may be by means of aplanospores. Sexual reproduction is by a fusion of biflagellate gametes that may be of equal or unequal size.

There are about 6 genera and 55 species, almost all of which are fresh-water.

Characium, a genus with about 40 species, usually grows upon other algae, submerged angiosperms, or various aquatic animals; but it may grow upon submerged woodwork or stones. The cells may be subspherical or ovoid, but more often they are elongated and fusiform or cylindrical. They are sessile and usually attached to the substratum by a more or less elongate stipe expanded into a small disk at the point of attachment to the substratum (Fig. 45*A*-*B*). The cells may grow isolated from one another, or they may be present in such abundance that they form a continuous stratum.

Young cells are uninucleate and with a parietal laminate chloroplast. As a cell grows older there may be a repeated nuclear division until 16, 32, 64, or 128 are present in the cell,[4] or the cell may remain uninucleate until just before reproduction.[5] Old cells frequently have a diffuse chloroplast containing more than one pyrenoid.

Asexual reproduction is by division of the protoplast into 8, 16, 32, 64, or 128 biflagellate zoospores (Fig. 46*C*). Multinucleate cells have a progressive cleavage of the cell contents into uninucleate protoplasts.[4]

[1] Cohn, 1872; Gardner, 1917; Kurssanow and Schemakhanova, 1927.
[2] Kurssanow and Schemakhanova, 1927. [3] Cohn, 1872.
[4] Smith, G. M., 1916. [5] Carter, Nellie, 1919*C*.

Cells that are uninucleate at maturity have a repeated division of the nucleus just before reproduction and a division of the protoplast after each mitosis.[1] The zoospores are liberated through an opening at the apex or at the side of the parent-cell wall. They may escape singly through the opening, or they may be discharged in a mass surrounded by a delicate vesicle. At the end of the swarming period a zoospore becomes affixed to some firm object, retracts its flagella, and secretes a wall.

When sexual reproduction takes place, there is a division of the protoplast into biflagellate gametes. In certain species the fusing gametes are quite different in size.[2]

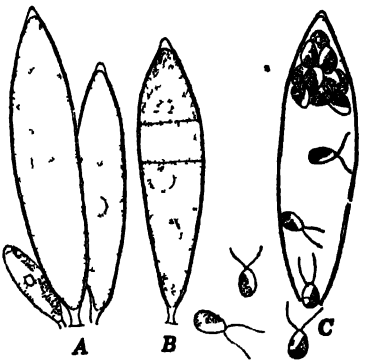


FIG. 46 — *Characium angustatum* A Br. *A*, vegetative cells. *B*, an early stage in cleavage to form zoospores *C*, liberation of zoospores The liberation at the basal end of the cell is abnormal and probably due to an accidental breaking of the cell wall. (× 650.)

FAMILY 4 PROTOSIPHONACEAE

The Protosiphonaceae have solitary, spherical to tubular, multinucleate cells in which one side may be prolonged into a colorless rhizoidal process The cells may contain a single large reticulate parietal chloroplast or many small parietal chloroplasts. Some genera produce zoospores. Others form biflagellate gametes only.

The family includes five genera, each with a single species. One is marine; the others are fresh-water.

Protosiphon, with the single species *P botryoides* (Kutz.) Klebs. usually grows on drying muddy banks of streams and ponds or on bare damp soil. It generally grows intermingled with *Botrydium*, one of the Xanthophyceae, quite similar in appearance. *Protosiphon* is a unicellular alga. Young plants are short erect tubes with the lower portion colorless; older plants have a broadly expanded globose to ovoid aerial green portion that is subtended by a narrow, colorless, simple or branched rhizoid which grows into the soil (Fig. 47*A*). The protoplasts are multinucleate and with a large vacuole in the aerial portion. The aerial portion contains a single large parietal chloroplast with several irregularly shaped perforations. Chloroplasts of mature cells contain several pyrenoids. The chief food reserve is starch.

Juvenile cells may multiply vegetatively[3] by sending out proliferous outgrowths and cutting off the proliferations by transverse septa (Fig. 47*B*). Flooding of plants growing on soil is soon followed by a division

[1] Carter, Nellie, 1919*C*. [2] Schiller, 1924. [3] Bold, 1933; Klebs, 1896.

of the entire protoplast into zooids.[1] The formation of zooids begins with an extrusion of water from the protoplast and its shrinking away from the cell wall. There then follows a progressive cleavage into uninucleate protoplasts as a result of an inward growth of furrows from the plasma and vacuolar membranes.[2] Each uninucleate protoplast is usually metamorphosed into a biflagellate zooid, but it may develop into a uninucleate aplanospore.

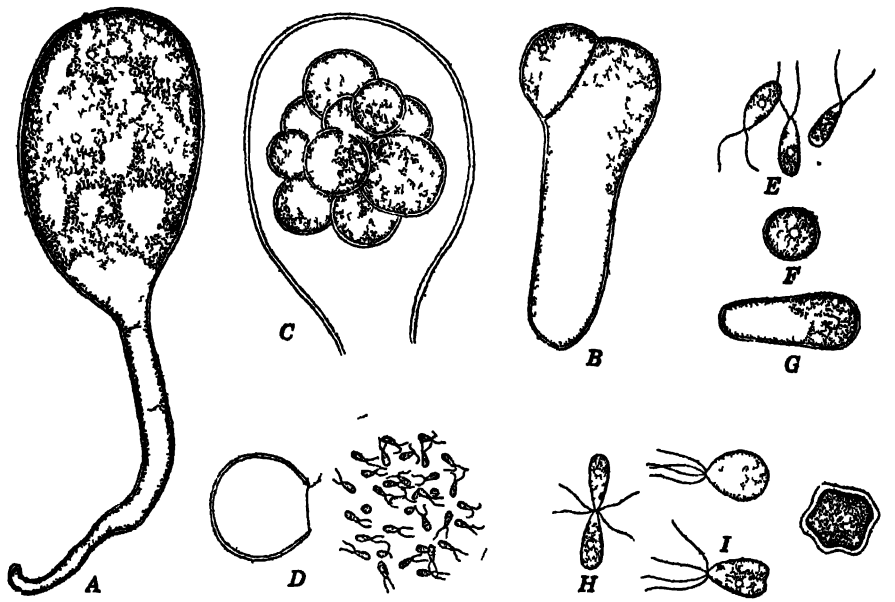


FIG 47.—*Protosiphon botryoides* (Kutz.) Klebs. *A*, mature vegetative cell. *B*, young cell cutting off a proliferation. *C*, aplanospores. *D*, germination of aplanospore. *E*, gametes. *F–G*, parthenogenetic germination of gametes. *H*, gametic union. *I*, young zygotes. *J*, mature zygote. (*A*, *C*, *D*, × 230, *B*, *E–J*, × 650.)

Thalli growing upon drying soil or in strongly illuminated places have the protoplast dividing to form a few or many multinucleate spore-like bodies (Fig. 47*C*). There is great variation in the size of these bodies formed within a single thallus. These aplanospores or "coenocysts" are produced by an inward furrowing of the plasma membrane.[2] The coenocytic aplanospores may develop directly into vegetative cells, but more frequently there is a progressive cleavage of their contents into biflagellate zooids (Fig. 47*D*).

Zooids of *Protosiphon* are gametic in nature, but they may germinate parthenogenetically and develop into vegetative cells (Fig. 47*E–G*). Some strains of *P. botryoides* grown in pure culture have proved to be

[1] Bold, 1933; Cienkowski, 1855; Klebs, 1896; Rostafiński and Woronin, 1877.
[2] Bold, 1933.

homothallic and others heterothallic.[1] There are also constant differences in structure of the gamete from strain to strain. Strains have been isolated[1] in which the gametes regularly lack an eyespot and pyrenoid, regularly have only an eyespot or a pyrenoid, or regularly have both. Fusing gametes[2] become apposed end to end and then fuse laterally to form a quadriflagellate zygote that swarms for a short time (Fig. 47*H–I*). When swarming ceases, the zygote retracts its flagella, becomes rounded, and secretes a thick stellately shaped wall (Fig. 47*J*). Fusion of the two gamete nuclei takes place quite early. The walled zygote enters upon a resting period before germinating directly into a vegetative cell. Studies on division of the zygote nucleus are inconclusive as to whether

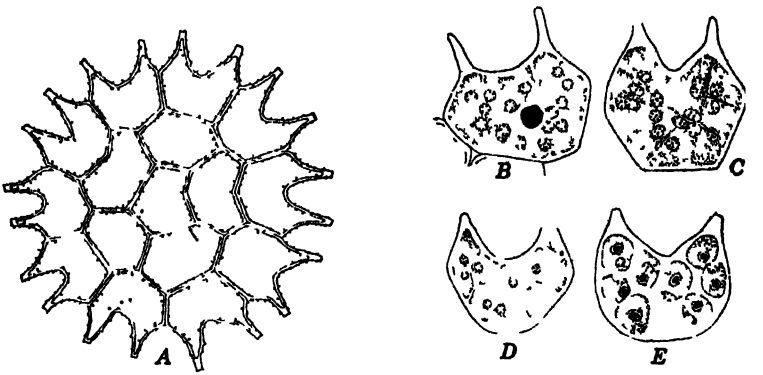


FIG 48 *Pediastrum Boryanum* (Turp.) Menegh. *A*, colony. *B*, cell just before cleavage into zoospores. (, progressive cleavage. *D–E*, after the completion of cleavage. (*A*, × 500, *B–E*, × 1,000.)

its division is equational or reductional.[3] Genetic analyses of plants produced by germinating zygotes indicate that nuclear division is reductional.[1]

FAMILY 5. HYDRODICTYACEAE

The Hydrodictyaceae have their cells united in free-floating colonies in which the number of cells is a multiple of two. The colonies are formed by an apposition of zoospores at the end of the swarming period. The swarming may take place within a gelatinous vesicle extruded from the parent cell, or the swarming zoospores may not escape from the parent-cell wall. Sexual reproduction is by a fusion of biflagellate gametes.

The family includes 4 genera and about 40 species, all fresh-water.

Pediastrum, with some 30 species, is a widely distributed alga that grows free-floating in pools, ditches, and the plankton of lakes. It rarely occurs in abundance. The colonies have 2 to 128 polygonal cells arranged in a stellate plate one cell in thickness (Fig. 48*A*). If a colony has 16 or

[1] Moewus, 1935. [2] Bold, 1933; Klebs, 1896. [3] Bold, 1933.

more cells, there is a tendency for the cells to be in concentric rings and to have a definite number in each ring. The occurrence or nonoccurrence of this regularity of arrangement is determined by factors affecting the extent to which zoospores swarm at the time a colony is formed.[1] Peripheral cells of a colony often differ in shape from interior cells. Peripheral cells may have one, two, or three processes; interior cells may or may not have them. Cell walls may be smooth, granulate, or finely reticulate. Walls of plankton species sometimes have long tufts of gelatinous bristles. Young cells have a single parietal chloroplast with one pyrenoid; old cells have a diffuse chloroplast that may contain more than one pyrenoid. Young cells are uninucleate; old cells may be bi- or quadrinucleate.[2]

Every cell in a colony (coenobium) is capable of giving rise to biflagellate zoospores, but there is rarely a simultaneous production of zoospores by all cells of a colony. The zoospores are produced during the night and are liberated shortly after daybreak. During the night before reproduction, there is a two- or a fourfold increase in the number of nuclei (Fig. 48*B*), followed by a progressive cleavage (Fig. 48*C E*) of the coenocyte into uninucleate protoplasts that are metamorphosed into zoospores.[2] The zoospores produced by a cell are surrounded by a vesicle as they escape from the old cell wall, and the vesicle persists throughout the period of swarming and for a short time after the new colony is formed.[3] The number of zoospores is dependent upon the physiological condition of the parent cell. For example, cells in a 16-celled colony may produce 4- or 8-celled daughter colonies, or they may produce daughter colonies with 32 or 64 cells. At the time zoospores are liberated, there is a sudden slit-like rupturing of the outer layer or the parent-cell wall and an extrusion of the spore mass surrounded by a sac-like vesicle (Fig. 49*A*). The vesicle is derived from the inner wall layer of the parent cell.[4] The zoospores swim freely and actively within the vesicle for the first three or four minutes following extrusion; after this they tend to arrange themselves in a flat plate (Fig. 49*B-D*) and to have their motion restricted to a writhing and twitching. Coincident with slowing down of movement, the zoospores begin to take on the shape of a vegetative cell, and cell walls are formed within a few minutes after swarming ceases.

In very rare cases the entire protoplast of a cell develops into a thick-walled aplanospore. These aplanospores (hypnospores) are extremely resistant to adverse conditions and have been known[5] to germinate after 12 years' desiccation.

[1] Harper, 1916, 1918, 1918*A*. [2] Smith, G. M., 1916*A*.
[3] Askenasy, 1888; Braun, 1851; Smith, G. M., 1916*A*. [4] Harper, 1918.
[5] Strøm, 1921*A*.

Pediastrum also produces biflagellate gametes that are formed in the same manner as zoospores.[1] They are spindle-shaped instead of ovoid and fuse in pairs to form a spherical zygote. After the zygotes have

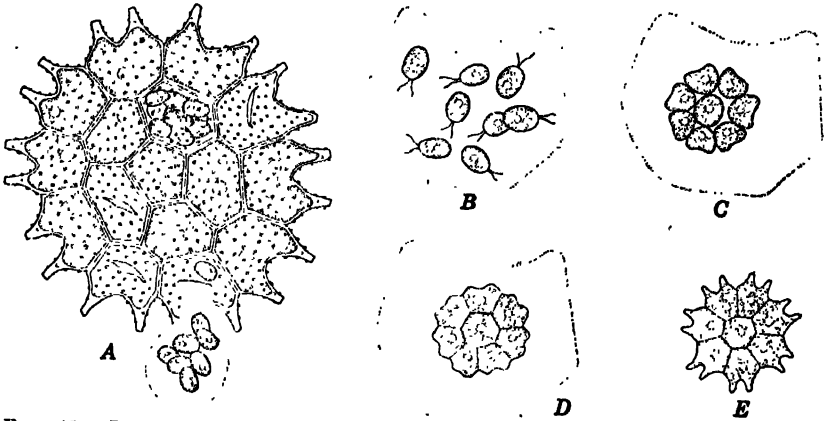


FIG. 49.—*Pediastrum Boryanum* (Turp.) Menegh. *A*, liberation of zoospores. *B*, swarming zoospores. *C–E*, stages in formation of a daughter colony. (*B* to *D* drawn at approximately 10-minute intervals.) (*A*, × 500; *B–E*, × 1,000.)

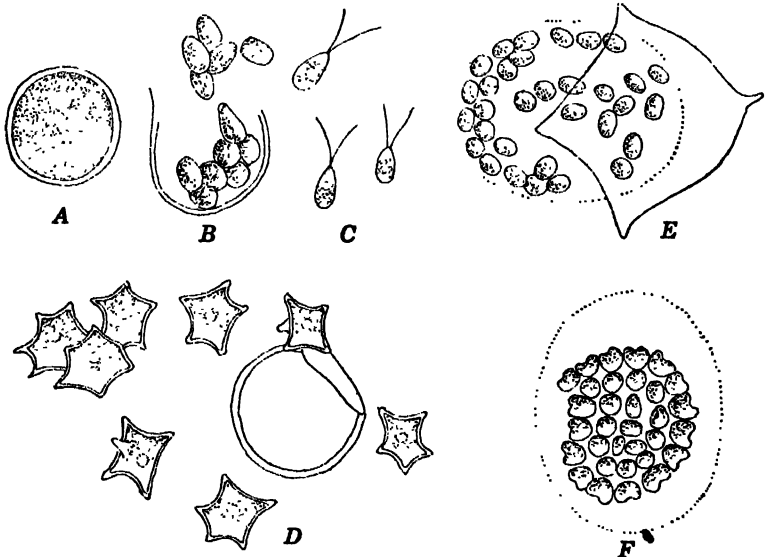


FIG. 50.—*Pediastrum Boryanum* (Turp.) Menegh. *A*, zygote. *B*, germinating zygote. *C*, zoospores. *D*, empty zygote and polyeders. *E–F*, germination of polyeder. (*After Palik*, 1933.) (*A–B*, × 495; *C*, × 750; *D*, × 800; *E–F*, × 525.)

increased greatly in size (Fig. 50*A*), their protoplasts divide to form a considerable number of biflagellate zoospores.[2] The zoospores are liberated through a large opening at one side of the zygote wall, and they swim freely in all directions after liberation (Fig. 50*B–C*). Upon coming

[1] Askenasy, 1888. [2] Palik 1933

to rest they develop into solitary angular cells (Fig. 50*D*). These "polyeders" also increase greatly in size before their protoplasts divide to form zoospores. Zoospores produced by polyeders are surrounded by a vesicle when liberated.[1] They remain within the vesicle and become apposed to one another to form a vegetative colony, just as in asexual reproduction (Fig. 50*E–F*).

FAMILY 6. OÖCYSTACEAE

The Oöcystaceae include all of the autosporic Chlorococcales in which the cells are solitary or in which the cells are united in colonies with an indefinite number of cells. There is no other method of reproduction other than a formation of autospores.

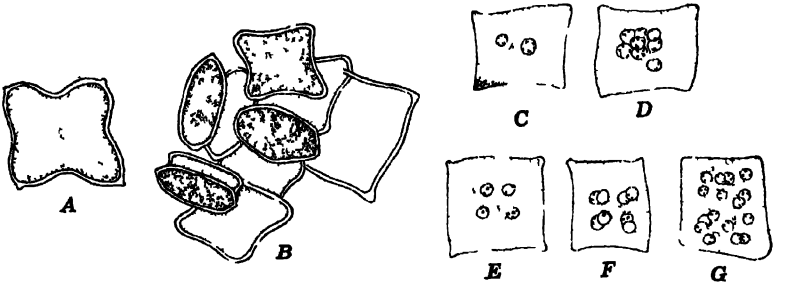


FIG. 51.—*Tetraedron minimum* (A Br) Hansg *A*, vegetative cell. *B*, liberation of autospores *C–G*, stages in formation of autospores (× 1500)

The family includes about 40 genera and 300 species. All species are fresh-water, and many of them are known only from the plankton.

Tetraedron is a unicellular genus with angular cells of various shapes. More than 60 species have been described, but many of them are open to suspicion since they have not been found producing autospores. Some of the questionable species may be resting stages of other green algae. Cells of *Tetraedron* (Fig. 51*A*) may be flattened or isodiametric, triangular, quadrangular, or polygonal. Angles of the cells may be simple or produced into simple to furcate processes. The cell wall is relatively thin, and smooth or verrucose. The cells may contain one to many discoid to angular parietal chloroplasts, or there may be a single chloroplast entirely filling the cell. Chloroplasts are with or without pyrenoids. Young cells are uninucleate; mature cells may contain two, four, or eight nuclei.[2]

Reproduction is by division of the protoplast into 2, 4, 8, 16, or 32 autospores (Fig. 51*B–G*). They are formed by repeated division of the protoplast and are immediately liberated by a rupture of the parent-cell

[1] Askenasy, 1888; Palik, 1933. [2] Smith, G. M., 1918.

wall. The reported reproduction by means of zoospores[1] is in need of confirmation.

FAMILY 7. SCENEDESMACEAE

The Scenedesmaceae include all of the Chlorococcales reproducing solely by autospores, in which the autospores become apposed to one another at the time of liberation to form a coenobium.

The family includes about 12 genera and 170 species, all fresh-water and many of them planktonic.

Scenedesmus, with about 100 species, is a widely distributed organism, and the algal flora of practically every body of standing water contains one or more species. It often appears in practically pure culture in

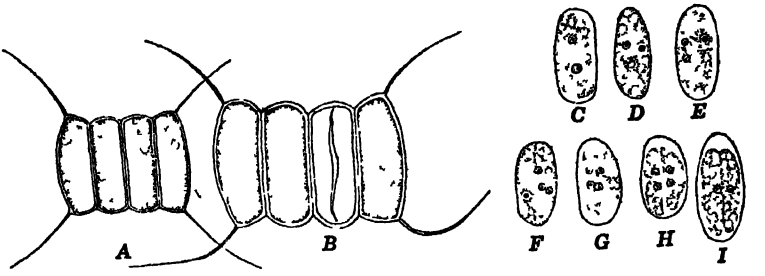


FIG. 52 —*Scenedesmus quadricauda* (Turp.) Breb. *A*, young colony. *B*, old colony in which one cell has produced and liberated a daughter colony. *C–I*, stages in formation of a daughter colony. (× 1,000.)

aquariums and in jars of water that have been standing in the laboratory for some time. The colony (coenobium) of *Scenedesmus* is a flat, rarely curved, plate of ellipsoidal to fusiform cells arranged in a single to double series with their long axes parallel to one another. The number of cells in a coenobium is always a multiple of two; usually 4 or 8, although sometimes 16 or 32. According to the species, the cell wall is smooth, corrugated, granulate, or spicate and is with or without terminal or lateral teeth or spines. Young cells have a single longitudinal laminate chloroplast containing one pyrenoid; chloroplasts of old cells usually fill the entire cell cavity (Fig. 52*A–B*). There is but one nucleus.

Each cell in a colony is capable of giving rise to a daughter colony, but there is rarely a simultaneous formation of daughter colonies by all cells in a colony. The number of cells in a daughter colony is partially dependent upon the physiological condition of the parent cell and may be smaller or greater than the number of cells in the colony to which the parent cell belongs. The protoplast of a cell about to form a daughter colony divides transversely, and the two daughter protoplasts divide vertically (Fig. 52*C–I*). This may be followed by one or two additional

[1] Probst, 1926.

series of vertical divisions.[1] The last generation of daughter protoplasts becomes autospores that remain laterally united to one another after their liberation by a longitudinal rupture of the parent-cell wall.

ORDER 10. SIPHONALES

The Siphonales are unicellular, multinucleate (coenocytic) algae in which the cell is generally a branched tube capable of indefinite elongation. The branching siphonaceous plant body of certain genera is amorphous. That of other genera has the branches definitely arranged upon an axis or has them intertwined to form a structure of definite macroscopic form. Relatively few members of the order produce zoospores or aplanospores. Almost all of them produce gametes, either in undifferentiated branches or in special gametangia. Sexual reproduction may be isogamous, anisogamous, or oögamous.

The order includes about 50 genera and 380 species. Most of the genera are marine and found in tropical or subtropical seas. All, or a large majority of, the species of a few genera are found only in fresh water. Three genera are parasitic.

The Siphonales intergrade with the coenocytic Chlorococcales, and it is a debatable question whether certain coenocytic Chlorophyceae, as *Protosiphon*, belong to the Chlorococcales or to the Siphonales.

The vegetative nuclei of many of the Siphonales are diploid, and in these algae there is a reduction division immediately before formation of gametes. However, one cannot say that this is characteristic of the entire order because there seem to be genera (for example, *Vaucheria*) in which meiosis takes place in the zygote and in which the vegetative phase of the life cycle is haploid.

The fossil record of the Siphonales is very fragmentary, but it is thought[2] that they go back as far as the Ordovician. In spite of the flimsy evidence, one is justified in assuming that the Siphonales are an ancient series because derivatives from them, the *Siphoneae verticillatae* (page 125) are well represented in the Ordovician.

The relationships between the present-day Siphonales are obscure. Those with the greatest complexity of vegetative differentiation (the *Caulerpas*) are least differentiated as far as reproductive structures are concerned. Conversely, the Vaucheriaceae have a very simple type of vegetative organization and the most advanced type of sexual reproduction. Because of these difficulties, it is impossible to determine which families are primitive and which are advanced.

The order is divided into six or seven families. These may be ranged in an ascending series according to increased complexity of vegetative

[1] Smith, G. M., 1914. [2] Pia, 1927.

structure or according to increased complexity of gametangia and type of gametic union. The latter is the usual method, but it is inadequate since sexual reproduction is unknown for two of the families.

FAMILY 1. BRYOPSIDACEAE

Thalli of Bryopsidaceae are unseptate and differentiated into a prostrate rhizome-like portion and an erect pinnately branched portion. Zoospores are unknown, but there may be an asexual reproduction by abscission of pinnules. Sexual reproduction is anisogamous, and the gametes are produced in pinnules of the erect branches or in outgrowths from them.

There are but 2 genera: *Bryopsis* with about 30 species, and *Pseudobryopsis* with a single species. Both genera are marine.

Most species of *Bryopsis* are found in warm seas, but a few of them grow in cold waters. The genus is widely distributed along both coasts of this country, but nowhere along either of them is it a common alga. The rhizome-like portion of the thallus appears to be perennial; it is uncertain whether the erect branches are annual or perennial. The erect axes are pinnately branched, and the pinnules may also be pinnately branched (Fig. 53*A*). Most species have the pinnules in two vertical rows along the erect axis, but some of them have pinnules arising on all sides of an axis. Since there is a continual abscission of fully developed pinnules, the lower half of an axis is generally devoid of appendages.

Internal to the cell wall is a layer of cytoplasm containing many nuclei and many small discform to spindle-shaped chloroplasts, each usually with a single pyrenoid (Fig. 53*C*). There is a large central vacuole internal to the cytoplasm. Vacuoles within pinnules are described[1] as continuous with that within the axis, but this is not true for the commonest Pacific Coast species, *B. corticulans* Setchell. The protoplasm within an old pinnule becomes separated from that within the axis by a broad gelatinous transverse wall. In *B. plumosa* (Huds.) C.A.Ag. this has been described[2] as arising through an ingrowth of the pinnule wall where it adjoins the axis. In *B. corticulans* there seems to be a transverse cleavage of the protoplasm at the base of a pinnule and a secretion of a gelatinous cross wall between the two newly formed plasma membranes. Later on, additional wall layers, similar in chemical composition to the lateral walls, are laid down on either face of the gelatinous wall (Fig. 53*E*). Sooner or later after formation of the cross wall, there is an abscission of the pinnule. In *B. corticulans* there is a conspicuous development of rhizoidal outgrowths at the pinnule base before this abscission takes place (Fig. 53*B*). Pinnules shed from an axis frequently develop into new thalli if conditions are favorable.

[1] Fritsch, 1935. [2] Mirande, 1913.

Sexual reproduction is anisogamous, and the gametes are biflagellate. On the Monterey Peninsula, California, *Bryopsis* fruits abundantly dur-

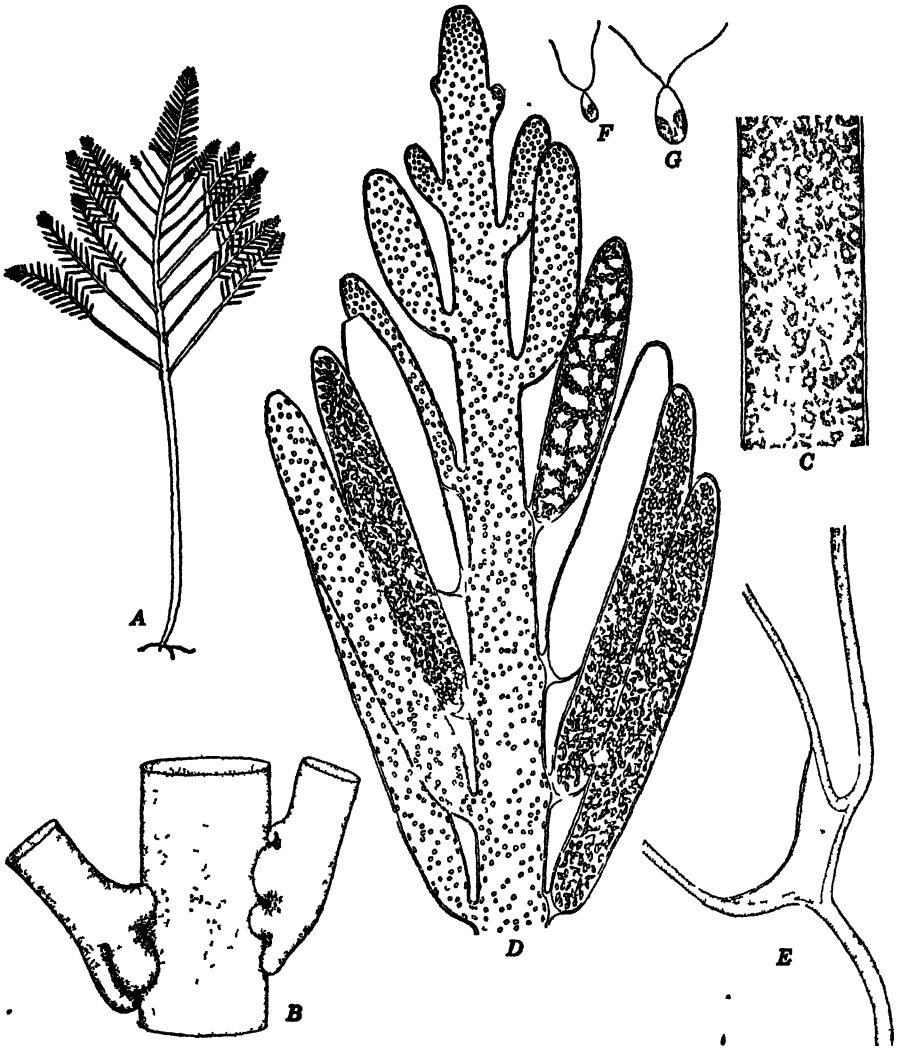


FIG. 53.—*Bryopsis corticulans* Setchell. *A*, portion of a thallus. *B*, basal portion of pinnules showing rhizoidal outgrowths after formation of cross walls *C*, chloroplasts within a pinnule. *D*, apex of a female plant with empty gametangia and gametangia containing gametes *E*, cross wall at the base of a gametangium F, male gamete. G, female gamete. (*A*, natural size, *B*, × 21, *C*, *E*, × 325, *D*, × 42; *F–G*, × 650.)

ing the spring and only occasionally during the summer. The same appears to be true for plants growing in European waters, since all investigators describing sexual reproduction[1] collected their material

[1] Mirande, 1913; Pringsheim, 1871; Zinnecker, 1935.

during the spring. Male and female gametes are produced upon separate plants. They are formed within unmodified pinnules separated from the main axis by a transverse wall. Occasionally there is also a formation of gametes within the axis. Fruiting male plants are macroscopically recognizable because of the yellowish color of the fertile pinnae (gametangia), and female plants because of the dark-green color of their gametangia.

Conversion of a pinnule into a gametangium begins with a formation of a basal transverse wall. This is formed in the same manner as are those of old vegetative pinnae. An increase in the number of nuclei follows, and it has been shown[1] that nuclear division is reductional. The protoplast then becomes divided into a large number of gametes that lie in a reticulate layer just within the gametangial wall (Fig. 53*D*). In *B. corticulans* the gametes, both male and female, escape through one or more small pores in the gametangial wall. The gametes swarm actively within the gametangium and escape singly through the pore. Emptying of a gametangium is a slow process and frequently lasts for more than an hour. Liberated gametes swarm for several hours, and under laboratory conditions those freed early in the morning are still actively motile late in the afternoon. Female gametes of *B. corticulans* (Fig. 53*G*) are pyriform, usually with two chloroplasts, and have a conspicuous eyespot. Male gametes are about a third as large and contain a single chloroplast (Fig. 53*F*). Gametic union is frequent when the two kinds are mixed with each other. The zygote soon becomes invested with a wall, and there is an early fusion of the two gamete nuclei.[1] The zygote germinates immediately but development into a new plant is slow and germlings four months old are but a few millimeters tall and without pinnules. Division of the zygote nucleus is equational, not reductional.[1]

FAMILY 2. CAULERPACEAE

The Caulerpaceae have a one-celled thallus with a rhizome-like portion bearing root-like appendages on its lower face and erect shoot-like appendages on its upper face. Asexual reproduction is by fragmentation of a thallus. Sexual reproduction is isogamous or anisogamous and by means of biflagellate gametes formed by division of the protoplasm within the upright shoots.

There is but one genus, *Caulerpa*. It has about 60 species; all are marine and almost all of them are restricted to warm seas. Approximately 15 species are known from Florida,[2] and several of them have been found growing at a depth of 75 to 80 meters. *Caulerpa* is not found along the Pacific Coast of this country.

[1] Zinnecker, 1935. [2] Taylor, 1928.

When classified upon an ecological basis[1] the species fall into the following three classes: (1) mud-collecting species growing epiphytically upon roots of mangroves, (2) sand- and mud-bottom species that may grow in shallow or in deep water, and (3) rock and coral-reef species.

The one-celled thallus of *Caulerpa* has a size and an external form comparable to that of a vascular plant with a creeping rootstock. The rhizome-like portion of a thallus and the rootlet-like rhizoids are much

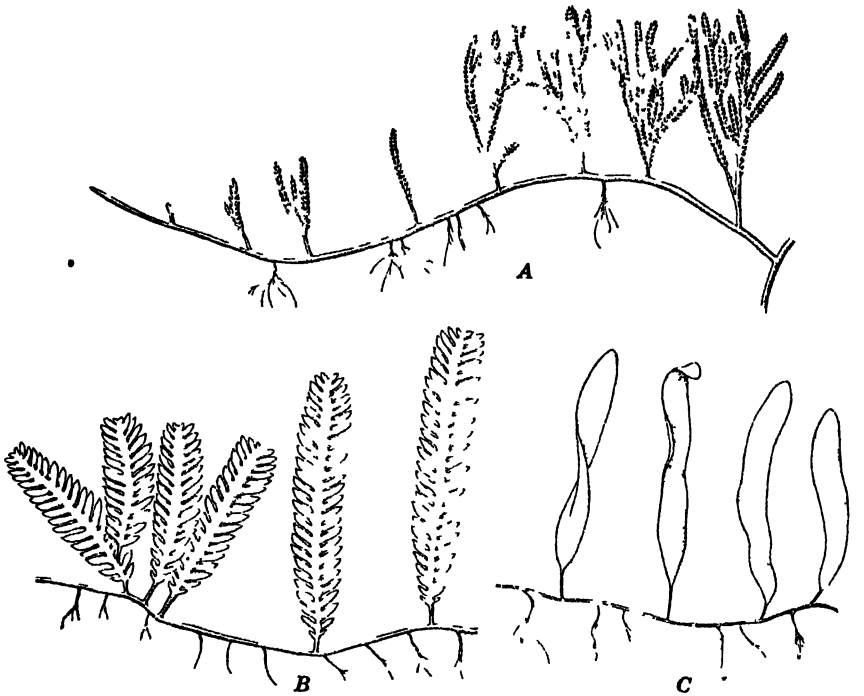


FIG. 54.—*A*, *Caulerpa cupressoides* (West) C.A.Ag. *B*, *C. crassifolia* (C.A.Ag.) J.G.Ag. *C*, *C. prolifera* (Forsk.) Lamx. (× ½.)

the same from species to species. There is great variation in form of the erect branches—the "leafy shoots"; and species have been named for the resemblance of their leafy shoots to cacti, to yews, to mosses, and to lycopods (Fig. 54). Mechanical support of the erect shoots is due to turgor and to thickness of the cell wall; not, as in certain other Siphonales, to an interweaving of branches or to an impregnation with lime. A thallus is without transverse walls, but there are numerous transverse and longitudinal rods (*trabeculae*) of callose and pectic materials (Fig. 55*A*). The function of the trabeculae is uncertain. Possibly they are mechanical supports that increase the rigidity of a plant. The multinucleate layer of cytoplasm internal to the wall contains many discoform chloroplasts without pyrenoids.

[1] Børgesen, 1907.

Asexual reproduction is effected by a fragmentation of a thallus or by an abscission of proliferous shoots.

Several species are now known[1] to produce biflagellate zooids. When growing in the Mediterranean, *C. prolifera* (Forsk.) Lamx. fruits during the autumn.[2] The production of zooids may be restricted to the foliar shoots, or it may also take place in the rhizome. The details of zooid formation are unknown, but, after zooids are formed, they tend to lie in reticulate masses within the cell. Formation of zooids is accompanied

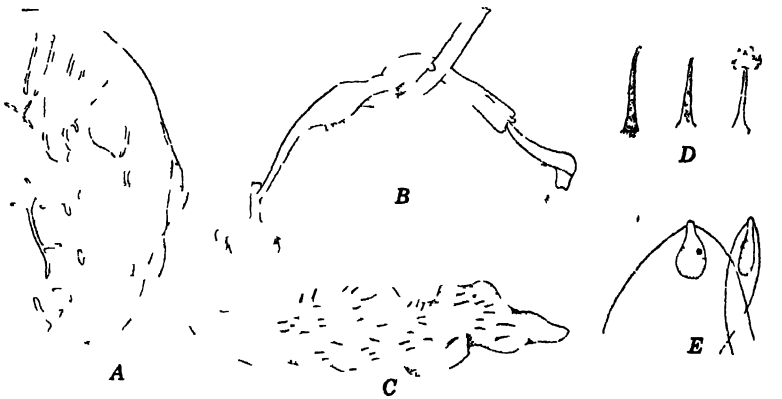


FIG. 55 *Caulerpa prolifera* (Forsk.) Lamx. *A*, transverse section of a rhizome. *B*, liberation of zooids. *C*, blade with exit papillae. *D*, development of exit papillae. *E*, zooids. (*A*, *B*, *E*, *after Dostal*, 1929, *C*, *D*, *after Schussnig*, 1929.)

by a development of numerous papillate outgrowths upon the surface of the thallus. These are extrusion papillae through which the zooids escape (Fig. 55*C–D*). Zooids are liberated through the extrusion papillae shortly after daybreak—sometimes in such quantity[3] that small green clouds appear in the water about a plant (Fig. 55*B*). The zooids are pyriform, biflagellate, and have a single chloroplast and a conspicuous eyespot (Fig. 55*E*). Gametic union has not been observed in *C. prolifera*. It has been observed[4] in several oriental species, and one of them [*C. clavifera* (Turn.) C.A.Ag.] has been shown to be dioecious and anisogamous. Germination of the zygote has not been followed. Fruiting of a plant is followed by a disintegration and disappearance of the empty portion of the thallus.

FAMILY 3. HALICYSTACEAE

The Halicystaceae differ from other Siphonales in that there is only a plasma membrane between the gametangium and the vegetative portion of a thallus.

[1] Dostal, 1928, 1929; Ernst, 1931; Iyengar, 1933*A*; Schussnig, 1929.
[2] Dostal, 1928, 1929; Schussnig, 1929. [3] Dostal, 1929.
[4] Ernst, 1931; Iyengar, 1933*A*

The single genus, *Halicystis*, is a marine algae with three or four species. It is widespread, although not common, along the Pacific Coast of this country and has been collected at the Dry Tortugas, Florida. The Pacific Coast species, *H. ovalis* (Lyngb.) Aresch., grows epiphytically upon calcareous Rhodophyceae, especially *Lithophyllum* and *Lithothamnion*.

The thallus is differentiated into a short erect colorless rhizome and a large globose green vesicle a centimeter or more in diameter (Fig. 56*A*). The rhizome grows directly downward into the substratum, the vesicle stands above it. The vesicle has a thick wall with many concentric layers.[1] Within the wall is a layer of protoplasm, and internal to this is a large central vacuole. At the inner face of the protoplasm are many small disciform chloroplasts without pyrenoids. The nuclei lie external to the chloroplasts (Fig. 56*C*). The wall of a rhizome is thinner than that of a vesicle, but it has many peg-like ingrowths. The rhizome is more or less completely filled with a multinucleate mass of cytoplasm containing many starch grains.

Thalli of *H. ovalis* are perennial; shedding their vesicles in the autumn and regenerating new ones each spring.[2] Late in the summer there is a formation of a cross wall at the juncture of vesicle and rhizome. Shortly afterwards there is a development of a transverse line of abscission across the basal region of the wall of the vesicle (Fig. 56*D*), which is followed by an abscission of the vesicle. The persistent rhizome becomes more deeply embedded in the substratum from year to year. This is due to an upgrowth of the host alga rather than to a downward growth of the rhizome into the alga.[1]

Reproduction of *Halicystis* is sexual and is effected by a fusion of biflagellate anisogametes.[3] The two kinds of gametes are produced on separate plants and in irregularly shaped gametangia darker in color than vegetative portions of a vesicle. Male plants have yellowish-tan gametangia; female plants have dark-green gametangia.[2] Fruiting of *H. ovalis* is periodic along the Pacific Coast, and gametes are produced and liberated during the spring tides of each lunar month.[4]

Development of a gametangium begins with a heaping up of protoplasm in radiate folds at one side of a vesicle (Fig. 57*A*). The folded region gradually smooths out into an area with a thickness six to eight times[1] that of a vegetative portion of a vesicle. The gametangial area also differs from vegetative portions in that chloroplasts and nuclei are uniformly distributed throughout it (Fig. 57*B*). A thin layer of protoplasm is then cut off on both the inner and outer faces of the

[1] Hollenberg, 1935. [2] Hollenberg, 1935; Kuckuck, 1907.
[3] Hollenberg, 1935; Smith, G. M., 1930. [4] Hollenberg, 1936.

gametangial area. This is effected by a lateral fusion of vacuoles developed just within the plasma and vacuolar membranes. The inner layer contains a few nuclei but no chloroplasts: the outer layer is thicker and contains both chloroplasts and nuclei. The multinucleate protoplasmic mass between the two layers cleaves progressively into uninucleate protoplasts (Fig. 57*C*), each of which is metamorphosed into a biflagellate gamete. Gametes within a gametangial area of a male plant are small, pyriform, with a single chloroplast (Fig. 57*D*). Those of female plants

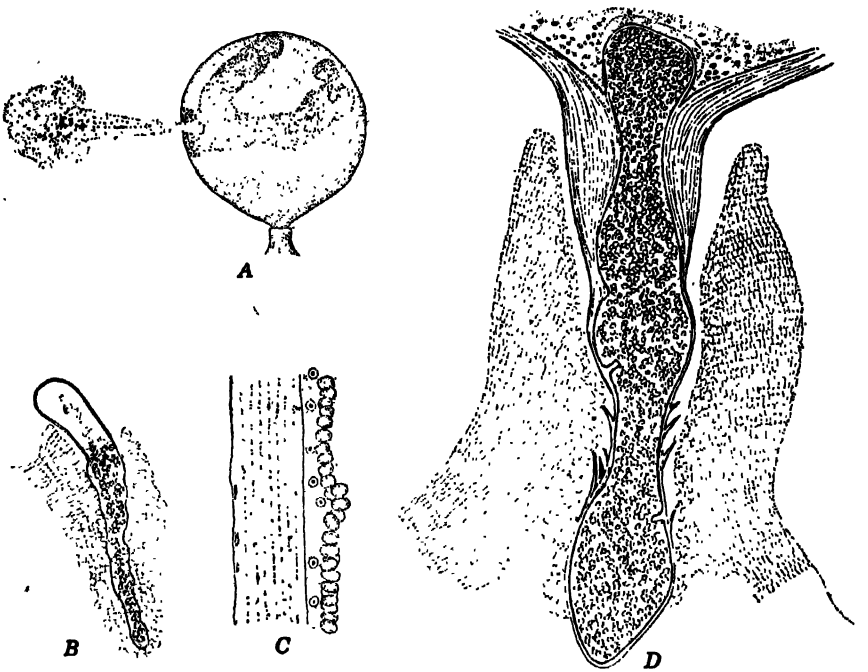


FIG. 56.—*Halicystis ovalis* (Lyngb.) Aresch. *A*, fertile plant liberating gametes. *B*, juvenile plant. *C*, vertical section of a portion of the vesicle. *D*, old rhizome with a cross wall at the juncture with vesicle. (*A*, × 5; *B*, *D*, × 80; *C*, × 650.)

are somewhat larger and contain several chloroplasts (Fig. 57*E*). Gametogenesis is accompanied by a localized gelatinization of several small areas in the cell wall external to the gametangium. These become the pores through which the gametes are discharged.

The gametes are forcibly and suddenly ejected shortly after day break.[1] Discharge of gametes from plants growing in aquariums may be delayed for two or three hours by keeping them in a dark room and then bringing them into the light. Discharge takes place within three or four minutes after plants are brought into daylight. The gametes are discharged in a green jet that extends from 20 to 40 mm. from an

[1] Hollenberg, 1935; Smith, G. M., 1930.

exit pore (Fig. 56*A*). The jet disperses within a few seconds and much like a puff of smoke. Discharge may be in a continuous stream or in several intermittent puffs. Intermittent discharge may be through the same pore or each successive jet may be through a different pore.

Gametic union follows immediately after discharge and a fusing pair have their anterior poles apposed to each other (Fig. 57*F*). The flagella disappear shortly after the gametes become apposed, and the zygote soon becomes spherical and secretes a wall. There is an immediate germination of a zygote and within a week the germ tube grows to a length four to six times the diameter of the zygote.[1] The germ tube develops into a *Vaucheria*-like protonematal stage, differentiated into prostrate and erect branches. Prostrate branches may elongate indefinitely; erect ones grow to but a limited height. The prostrate branches put forth rhizoidal branches that penetrate the coralline alga by digesting vertical rows of its cells. After a rhizoid has become well established within the underlying alga, there is a formation of a cross wall between the embedded portion and that above the alga. This is eventually followed by a disappearance of the superficial portion of the protonema.[1] The

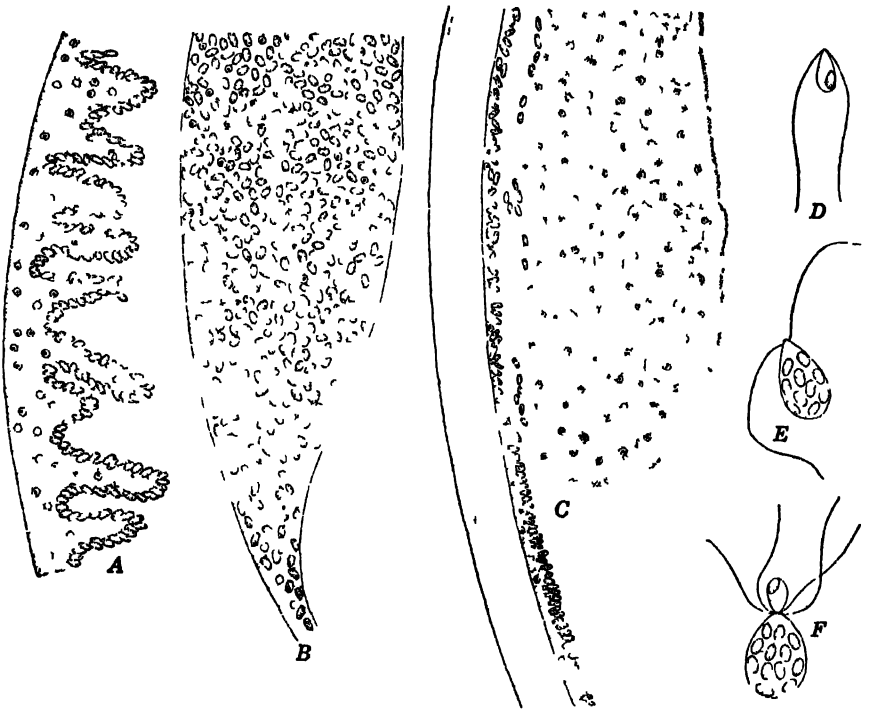


FIG. 57.—*Halicystis ovalis* (Lyngb.) Aresch. *A*–*C*, development of a female gametangium. *D*, male gamete. *E*, female gamete. *F*, gametic union. (× 650.)

[1] Hollenberg, 1935

persistent rhizoidal portion, now a young rhizome, then produces a small vesicle at its distal end (Fig. 56*B*). Further development is at a very slow rate, and it is very probable that a plant does not fruit until it is four or five years old.

FAMILY 4. CODIACEAE

The Codiaceae have a freely branched tubular thallus in which the branches are interwoven to form a plant body of definite macroscopic form. Reproduction is sexual, anisogamous, with the gametes produced in gametangia of distinctive shape.

The family includes some 16 genera and 120 species. All species are marine, and a very large majority of them are restricted to warm seas.

Codium, a genus with about 45 species, is found along the entire Pacific Coast of this country and as far north as North Carolina on the Atlantic Coast. The much-branched tubular thallus may have the branches interwoven into a prostrate cushion-like mass, into a spherical mass, or into an erect cylindrical body with several successive dichotomous branchings (Fig. 58*A*). Erect cylindrical portions of a thallus have an axial core of densely interwoven colorless filaments from which arise lateral branchlets, the *utricles*, that lie in a palisade-like layer about the central axis (Fig. 58*B*). Each utricle has a large central vacuole and a fairly thick layer of protoplasm between the vacuole and the cell wall. The chloroplasts, which are discoform and without pyrenoids, lie just within the plasma membrane, and most of them are at the distal end of the utricle (Fig. 59.1). The nuclei are minute and numerous, and lie internal to the chloroplasts. Filaments of the axial core become blocked off here and there by an annular ingrowth of the cell wall. These thick transverse septa are especially numerous near bases of utricles.

Reproduction of *Codium* is sexual and the club-shaped gametangia are developed laterally upon the utricles.[1] Two gametangia are usually formed upon a utricle, but development of the two is not simultaneous. Some species, including the common one along the Pacific Coast—*C. fragile* (Suring.) Hariot—are strictly dioecious; other species have[2] occasional monoecious individuals. On the Monterey Peninsula, California, *C. fragile* fruits throughout the year but most abundantly during the summer.

Gametangial development begins with the outgrowth of a tubular projection at one side of a utricle. A developing gametangium is solidly filled with cytoplasm in which the nuclei are evenly distributed, and the chloroplasts tend to aggregate at the distal end. When a gametangium is about two-thirds developed, there is an annular thickening of the wall

[1] Thuret, 1850. [2] Schmidt, 1923.

about its base. This completely separates the gametangial protoplast from that in the utricle. Some of the nuclei within a gametangium degenerate; others enlarge and divide meiotically into four daughter nuclei.[1] Beginning at the basal end, there is next a progressive cleavage into uninucleate protoplasts Female gametangia contain a few hundred uninucleate protoplasts; male gametangia a few thousand. Each

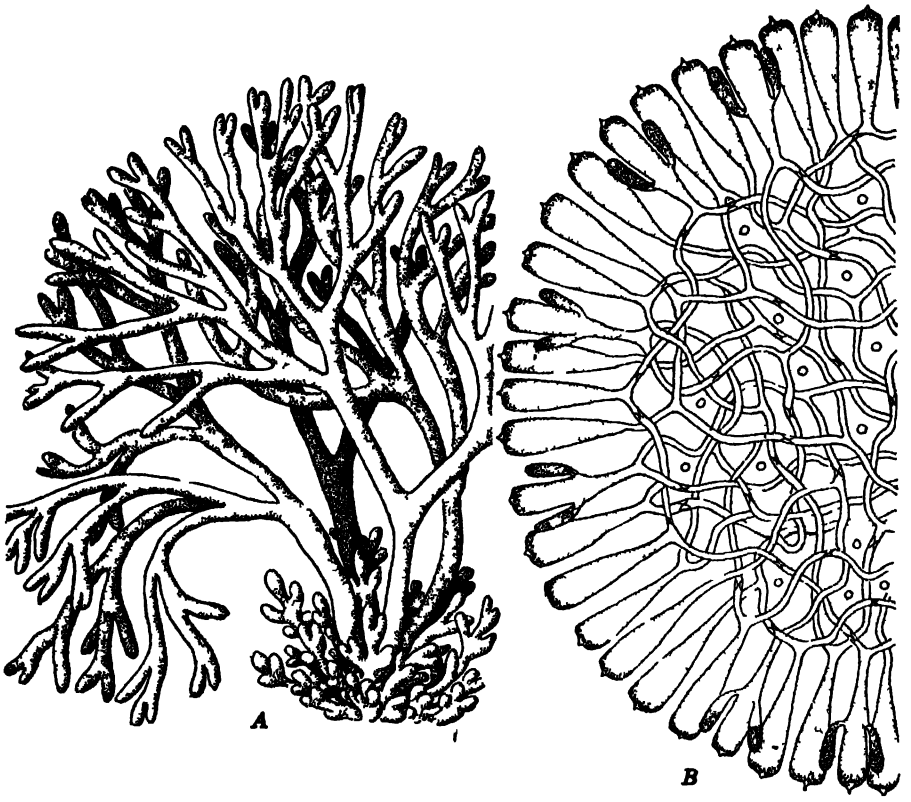


FIG 58.—*Codium fragile* (Suring) Hariot *A*, thallus *B* diagrammatic transverse section of a thallus (*A*, × ½, *B*, × 21)

uninucleate protoplast is then metamorphosed into a biflagellate gamete. Male gametes are pyriform and contain one or two chloroplasts; female gametes are several times larger and contain many chloroplasts (Fig. 59*E-F*) Male and female gametangia may be distinguished from each other even before the gametes are formed because of the golden-yellow contents of the former and the dark-green contents of the latter.

C. fragile grows in the intertidal zone, and its gametes are discharged when thalli are reflooded by the incoming tide. Gametic discharge seems to be due to an imbibitional swelling of gelatinized inner layers of

[1] Schussnig, 1930; Williams, 1925

the gametangial wall. Discharge begins[1] with a rupture of the lid-like portion of the gametangial apex. There is next an extrusion of a solid

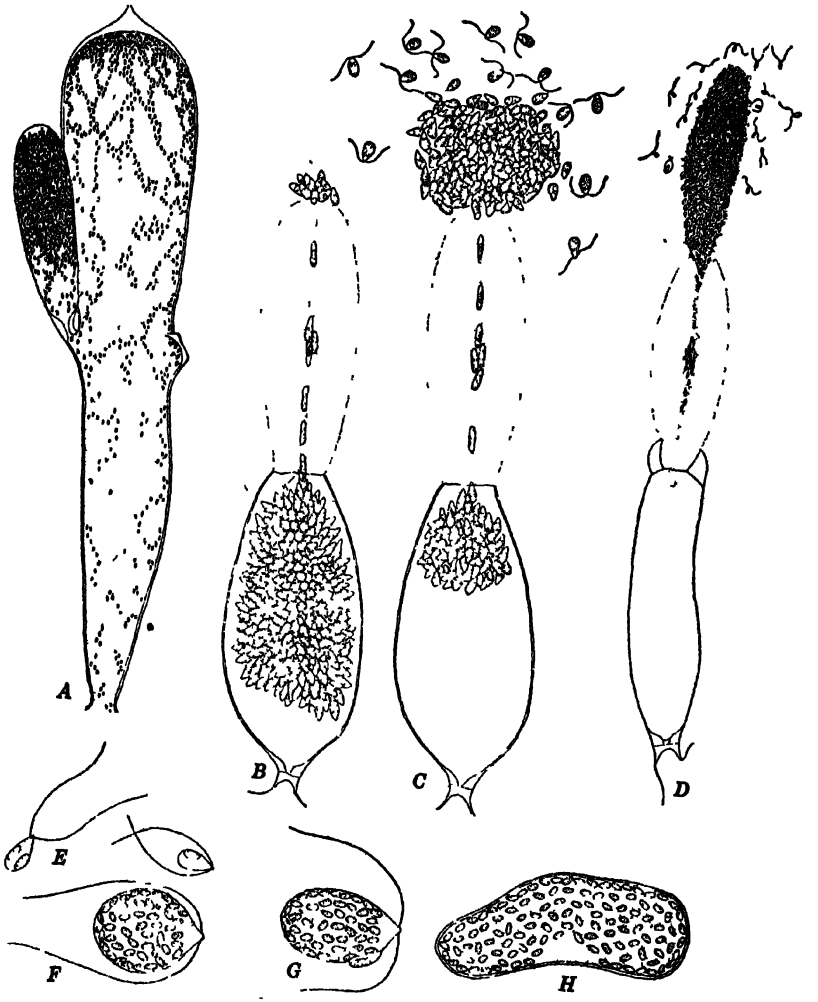


FIG. 59.—*Codium fragile* (Suring.) Hariot. *A*, utricle with a young female gametangium. *B–C*, female gametangia liberating gametes. *D*, male gametangium liberating gametes. *E*, male gametes. *F*, female gamete. *G*, gametic union. *H*, germination of zygote. (*A*, × 100; *B–C*, × 175; *D*, × 150; *E–H*, × 600.)

gelatinous mass of much the same size and shape as the gametangium. There is an axial canal within the gelatinous mass and the gametes exude rapidly through this canal and accumulate at its free end.[1] Movement of gametes through the canal is purely passive (Fig. 59*B–D*) and is

[1] Borthold in Oltmanns, 1922; G. M. Smith, 1930.

due to hydrostatic pressure within the gametangium. The passive nature of gametes during discharge is shown both by their lack of flagellar movement and by their being squeezed to a narrower diameter while being ejected through the canal. Ejection of gametes is rapid and usually takes less than a minute. Flagella become evident on gametes that have moved through the canal, and within a minute or two the lashing back and forth of the flagella propels the gamete away from the heap accumulated at the mouth of the canal.

Gametic union (Fig. 59*G*) takes place while both gametes are actively motile. A male gamete becomes applied to the side of a female gamete, loses its flagella, and gradually fuses with the female gamete.[1] Flagella of female gametes persist for a time after gametic union, but they soon disappear and the zygote assumes a spherical shape and secretes a wall. There is an immediate germination of a zygote, but further development is slow and germlings three weeks old are not more than four or five times their original length (Fig. 59*E*). Somewhat older germlings are *Vaucheria*-like and sparingly branched.[2] Certain lateral branches of this protonema-like stage enlarge greatly and become the first-formed utricles.[3] Additional utricles are formed as growth continues, and there is a gradual assumption of the organization characteristic of the adult thallus.

FAMILY 5. DERBESIACEAE

The Derbesiaceae differ from other Siphonales in that they produce zoospores similar to those of Oedogoniales. Several zoospores are formed within a sporangium. The thallus is a branched tubular coenocyte with the branches free from one another.

There are two genera with about a dozen species, all of them marine.

The relationships of the family are obscure, but the annular septa and the structure of the protoplast point to a relationship to Bryopsidaceae and Codiaceae.

Derbesia has been found at isolated stations along both coasts of this country. The thallus is a freely branched coenocyte differentiated into a prostrate densely interwoven basal portion and a tuft-like erect portion. Branching of the erect portion is frequently dichotomous and sometimes with an unequal elongation of the dichotomies that results in a distinctly monopodial appearance (Fig. 60*A*). Older branches may be separated from the remainder of the filament by broad transverse septa. These develop as localized annular thickenings of the lateral walls.[4]

There is a thin layer of cytoplasm just within the cell wall, and internal to this is a large central vacuole. At the inner face of the cytoplasm

[1] Berthold in Oltmanns, 1922; G. M. Smith, 1930.
[2] Berthold in Oltmanns, 1922. [3] Tobler, 1911. [4] Mirande, 1913.

are many small discifonn to spindle-shaped chloroplasts with or without pyrenoids. The chloroplasts may lie parallel to, or stand perpendicular to, the vacuolar membrane The portion of the cytoplasm external to the chloroplasts contains many small nuclei

The zoospores are produced within sporangia borne laterally upon the erect filaments [1] Very young sporangia look like initials of branches,

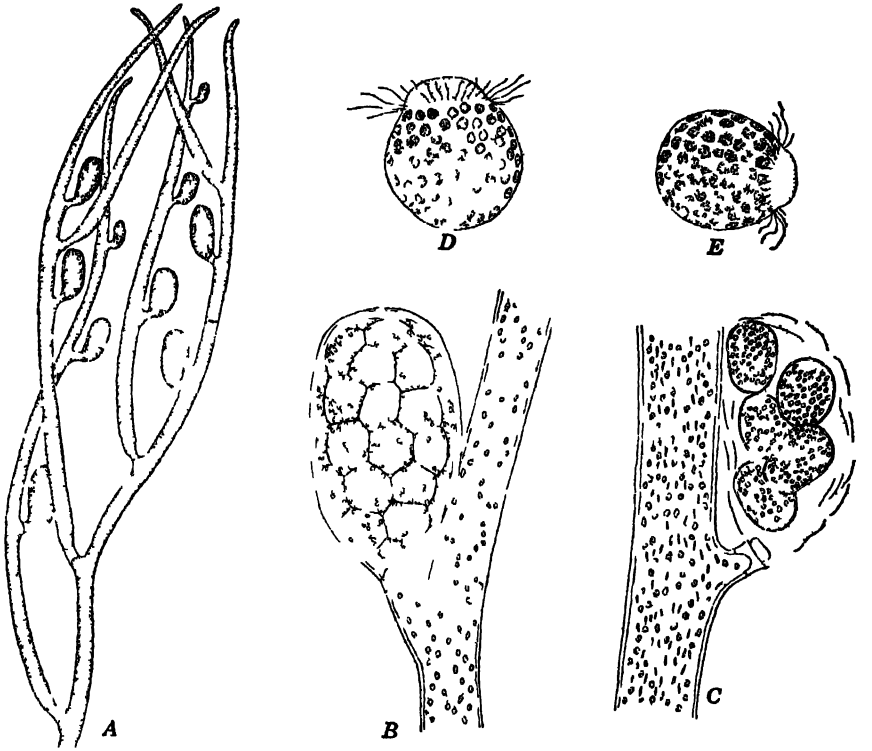


FIG 60 —*Derbesia marina* (Lyngb) Kjellm *A* portion of a thallus *B*, sporangium containing zoospores *C* sporangium containing aplanospores *D E*, zoospores (*A*, × 30, *B C* × 325 *D I* × 650)

but they soon become ovoid and elongate but little When the sporangia are about half grown, there is a formation of a transverse basal septum by an annular ingrowth of the lateral wall Developing sporangia have been described[2] as containing thousands of nuclei, but, in one of the species found along the Pacific Coast, *D marina* (Lyngb) Kjellm , there are not more than 200 or 300 Certain of the nuclei degenerate; the others enlarge to four to six times their original diameter There is a progressive cleavage of the sporangial contents into uninucleate protoplasts by an inward furrowing of the plasma membrane Each protoplast is metamorphosed into an ovoid zoospore (Fig. 60*D–E*) with a transverse

[1] Davis, 1908; Solier, 1847 [2] Davis, 1908

whorl of flagella at one pole. The flagella are produced by a ring-shaped blepharoplast just within the plasma membrane.[1] A sporangium contains 10 to 50 zoospores (Fig. 60*B*), and they are liberated by an irregular rupture of the sporangial wall. The zoospores swarm actively for several hours; then they come to rest, withdraw their flagella, secrete a wall, and germinate directly into a new filament. Occasionally there may be a secretion of walls about zoospores within an unopened sporangium. These aplanospores are liberated by a disintegration of the sporangial wall (Fig. 60*C*).

Derbesia has never been found reproducing sexually.

FAMILY 6. VAUCHERIACEAE

The Vaucheriaceae have a sparingly branched tubular thallus in which the branches are not intertwined. Asexual reproduction may be by zoospores or by aplanospores, both produced singly within a sporangium. Sexual reproduction is oögamous and with the oögonium containing a single egg that remains within it after fertilization.

There are 4 genera and about 40 species. Almost all of them are fresh-water in habit.

Vaucheria is a genus with some 35 species; three or four marine, the remainder fresh-water and terrestrial, or aquatic. Terrestrial species grow upon damp bare soil and in ploughed fields where they may form extensive green felty layers. The thallus is a sparingly branched tube that frequently attains a length of several centimeters. The thalli increase in length by apical growths and in most cases they are attached to the substratum by means of rhizoid-like branches with relatively few chloroplasts. The cell wall is relatively thin. Within the cell is a single central vacuole that runs without interruption the whole length of the coenocyte. The layer of cytoplasm between wall and vacuole contains chloroplasts toward its outer face and nuclei toward its inner face. The chloroplasts are small, circular to elliptical in outline, and without pyrenoids. *Vaucheria* differs physiologically from other Siphonales in that its carbohydrate food reserves are stored as oil instead of as starch. This lack of starch has been one of the chief arguments for placing *Vaucheria* among the Xanthophyceae,[2] but the fact that it may produce starch when continuously illuminated[3] and the fact that certain other members of the Vaucheriaceae regularly form starch shows that *Vaucheria* belongs to the Chlorophyceae.

Asexual reproduction may take place in a variety of ways. The commonest method is by means of large multiflagellate zoospores. All of the aquatic species form zoospores, and the terrestrial species form them

[1] Davis, 1908. [2] Blackman and Tansley, 1902; Bohlin, 1901.
[3] Tiffany, 1924.

when flooded. Zoospore formation may be induced in aquatic species by transferring them from light to darkness or from running to quiet water.[1] Zoospores are formed singly within club-shaped sporangia. Sporangial development begins with a club-shaped swelling of the distal end of a branch. There are many nuclei and chloroplasts in this inflated portion. There is next a transverse division of the protoplast, a short distance

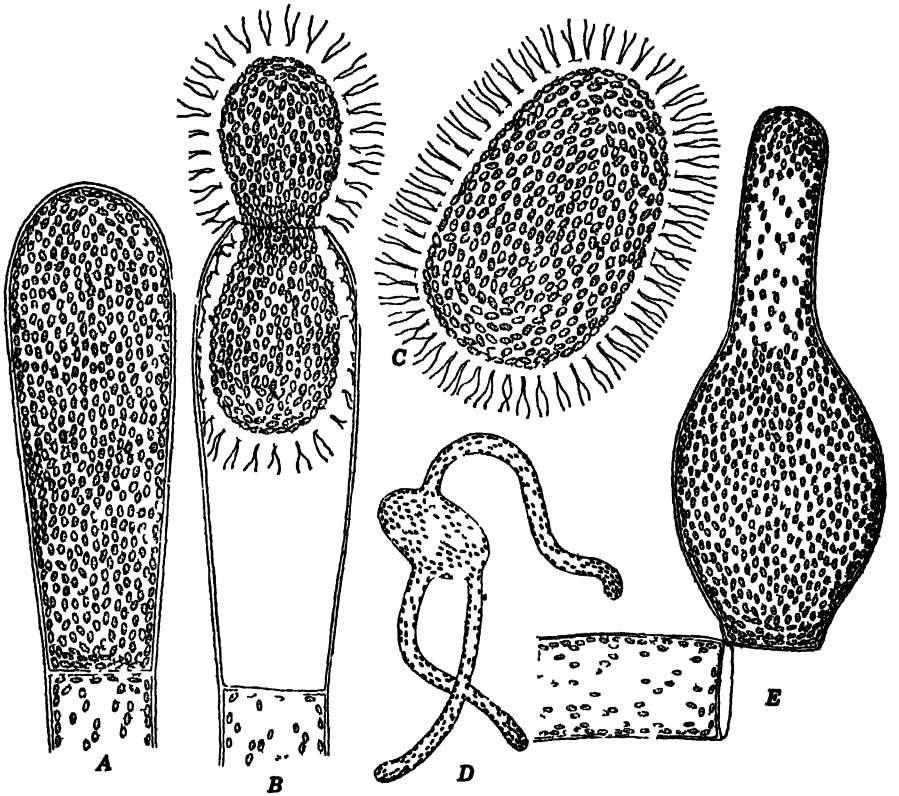


FIG. 61.—*Vaucheria* sp. *A*, zoosporangium *B*, liberation of zoospore. *C*, zoospore. *D*, germination of zoospore *E*, germination of a sporangium that has become an akinete. (*A–C*, diagrammatic) (*A–C*, × 430, *D*, × 60, *E*, × 325)

back from the branch apex, and a development of a transverse wall between the two newly formed plasma membranes (Fig. 61*A*). Nuclei and chloroplasts within a sporangium reverse their position so that the nuclei lie just within the plasma membrane. Following this, the protoplast contracts slightly and develops a pair of flagella external to each nucleus[2] or external to nuclei in the anterior half of a sporangium.[3] After the zoospore is fully developed, the distal portion of the sporangial wall softens to form a pore smaller in diameter than the zoospore. Libera-

[1] Klebs, 1896. [2] Strasburger, 1880. [3] Götz, 1897.

tion of zoospores usually takes place shortly after daybreak. A zoospore[1] squeezes its way through the narrow pore and then swims freely in all directions (Fig. 61*B–C*). It moves slowly through the water for 15 to 30 minutes; then it comes to rest, withdraws its flagella, and secretes a wall. Germination takes place immediately by a sending forth of from one to three tubular outgrowths that may elongate indefinitely (Fig. 61*D*). The multiflagellate zoospore of *Vaucheria* is generally interpreted as a compound zoospore formed within a sporangium in which there has been a permanent obliteration of cleavage of the sporangial protoplast into uninucleate biflagellate spores.

Terrestrial species frequently have the entire contents of a sporangium developing into a thin-walled aplanospore or a thin-walled akinete, instead of into a zoospore. Production of these nonflagellated spores is largely dependent upon environmental conditions since there is a regular formation of zoospores when the species grows submerged. The aplanospores are liberated by an irregular rupture of the sporangial wall; the akinetes may become detached from a thallus, or they may germinate while attached to it (Fig. 61*E*). Terrestrial species may also have a transverse segmentation of the entire protoplast into short segments and the secretion of a thick wall about each segment. Formation of these thick-walled aplanospores (hypnospores) is generally ascribed[2] to a drying out of the substratum, but in California[3] they are formed during the winter rainy season only when temperatures are near the freezing point. The hypnospores may germinate directly into a new filament, or their contents may divide into a number of thin-walled "cysts." The protoplast of a germinating cyst escapes through a pore in the wall and moves about in an amoeboid fashion. When amoeboid movement ceases, the protoplast assumes a spherical shape, secretes a wall, and develops directly into a filament.[2]

All species reproduce sexually. Sexual reproduction is of frequent occurrence among thalli growing on damp soil or in quiet water but is rarely found among plants growing in flowing water. All of the fresh-water species are homothallic; two or three of the marine species are heterothallic. Homothallic species bear their antheridia and oogonia adjacent to one another, either on a common lateral branch or on adjoining branches.

Antheridia are formed at the ends of short lateral branches and their development begins slightly before that of the oögonia. Most of the common fresh-water species have a hook-shaped antheridium opening by a terminal pore, but there are certain fresh-water species in which there is more than one pore and in which the antheridium is not hook-shaped.

[1] Birckner, 1912; Gotz, 1897; Klebs, 1896. [2] De Puymaly, 1922; Stahl, 1897.
[3] Smith, G. M , 1933.

The distal end of a branch producing an antheridium is more or less densely filled with cytoplasm containing many nuclei and a few chloroplasts (Fig. 62*A–B*). There is a transverse cleavage separating this portion of the protoplast from that in the remainder of the branch and a formation of a transverse wall between the two newly formed plasma membranes (Fig. 62*C*). The protoplast of an antheridium becomes divided into a number of uninucleate fragments each of which is metamorphosed into a biflagellate antherozoid. The insertion of the flagella is usually described[1] as lateral, but they have recently been found[2] to be terminal in insertion and of equal length. Antheridial development begins in the afternoon, and the formation of antherozoids is completed before daybreak the next morning.[3]

In species with the sex organs borne adjacent to one another, as *V. sessilis* (Vauch.) DC., oögonial development begins with an accumulation of a colorless multinucleate mass of cytoplasm in the main thread and near the base of an antheridial branch.[1] This is the "wanderplasm," and it moves into the young oögonium produced by a lateral bulging of the main thread (Fig. 62.1 *B*). Many nuclei and chloroplasts migrate into the oogonial bulge as it increases in size. The oögonial bulge eventually becomes an oögonium separated from the main filament by a transverse wall. The oögonium contains a single uninucleate egg. Descriptions of oögonial development are at variance. It has been held[4] that the uninucleate condition of the egg is due to a degeneration of all except one nucleus of a developing oögonium, but there seems to be more evidence supporting those[5] who hold that all but one, or all but a very few, of the nuclei migrate out from an oögonium before formation of the cross wall. In any case, it is quite clear[6] that the cross wall is not formed until very late in oögonial development (Fig. 62*C*).

Antherozoids enter an oögonium through an apical pore produced by gelatinization of the oogonial wall. Antherozoids are liberated shortly before daybreak,[7] and fertilization follows immediately afterward. Several antherozoids may enter an oogonium, but only one of them penetrates the egg. The small male nucleus migrates to the egg nucleus, which is considerably larger, but does not immediately fuse with it. The male nucleus increases in size until its volume approximates that of the egg nucleus; the two then fuse.[8] The fusing nuclei usually lie a short distance from the pore in the oögonial wall; the zygote nucleus formed by their fusion migrates to the center of the zygote.[4] The zygote

[1] Couch, 1932; Oltmanns, 1895. [2] Gross, 1937. [3] Couch, 1932.
[4] Davis, 1904; Mundie, 1929; Williams, 1926.
[5] Couch, 1932; Gross, 1937; Heidinger, 1908; Oltmanns, 1895.
[6] Couch, 1932; Mundie, 1929. [7] Couch, 1932; Mundie, 1929; Oltmanns, 1895.
[8] Mundie, 1929; Williams, 1926.

secretes a thick wall, with three to seven layers, and its protoplast becomes densely filled with oil (Fig. 62*D*). The zygote generally enters

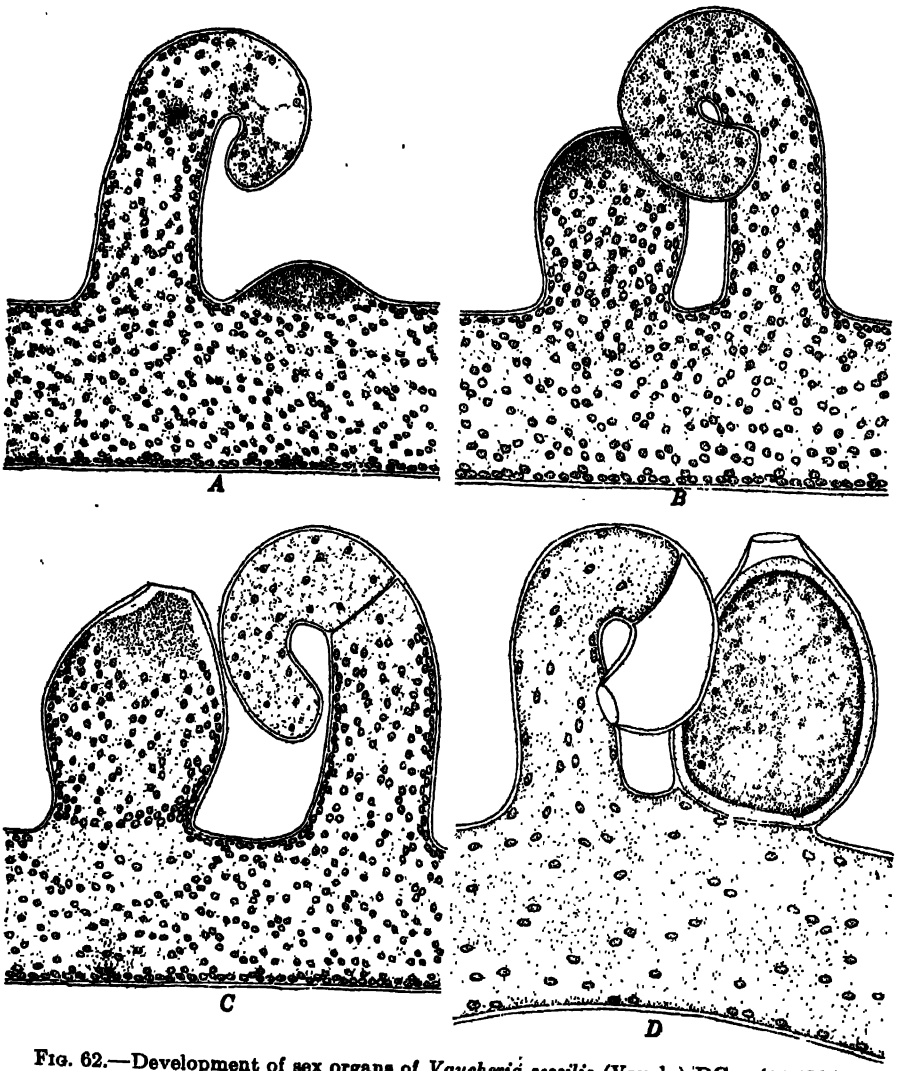


FIG. 62.—Development of sex organs of *Vaucheria sessilis* (Vauch.) DC. (× 430.)

upon a resting period of several months before it germinates directly into a new filament.[1] The rather inconclusive data indicate[2] that division of the zygote nucleus is meiotic.

[1] Mundie, 1929; Pringsheim, 1855; Walz, 1866.
[2] Gross, 1937; Hanatschek, 1932; Williams, 1926.

FAMILY 7 PHYLLOSIPHONACEAE

The Phyllosiphonaceae are endophytic or endozoic and with a tubular or vesicular coenocytic thallus The only known method of reproduction is a formation of aplanospores

There are 3 genera with 10 species

Phyllosiphon grows as an intercellular parasite in the stems and leaves of various Araceae There are five species, and one of them, *P Arisari* Kuhn, has been collected[1] in Wisconsin and in New Hampshire growing

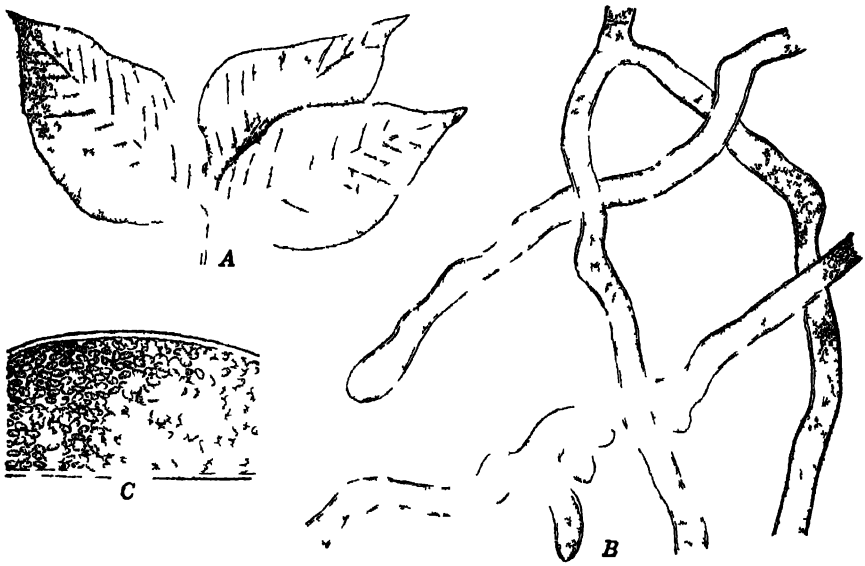


FIG 63.—*Phyllosiphon Arisari* Kuhn *A* leaf of *Arisaema triphyllum* (L.) Schott infected with *Phyllosiphon* *B*, *C* portions of thallus of *Phyllosiphon* (*A* × 1; *B*, × 160, *C*, × 650)

parasitically upon the jack-in-the-pulpit [*Arisaema triphyllum* (L.) Schott] The parasitism of the alga hinders development of chloroplasts by the host, hence the yellowish-green color of areas infected by the alga (Fig 63 *A*) Later, the presence of the parasite stimulates a secretion of yellowish-orange droplets of oil within cells of the host Still later, the presence of the alga may cause a disappearance of the color from the entire leaf except where the *Phyllosiphon* filaments are interwoven to form a green mat

The thallus of *Phyllosiphon* is a dichotomously or irregularly branched tube, in which branching is profuse and the various branches are loosely interwoven with one another (Fig 63*B*, *C*) The entire coenocyte is densely packed with ellipsoidal chloroplasts, except at the tips of growing

[1] Smith, G M, 1933 [2] Maire, 1908

branches. The chloroplasts are without pyrenoids and may form either starch or oil.[1]

Reproduction is by the formation of many small ellipsoidal aplanospores within all portions of the coenocyte.[2] The aplanospores germinate directly into new thalli.[3]

ORDER 11. SIPHONOCLADIALES

The Siphonocladiales have a thallus that is siphonaceous when young, but which later becomes partitioned into a number of multinucleate segments. Vegetative multiplication is of frequent occurrence, but there is rarely an asexual reproduction by means of zoospores. Most members of the order reproduce sexually by a fusion of biflagellated isogametes.

All members of the order are marine and usually restricted to tropical and subtropical seas. There are about 25 genera and 120 species.

As originally delimited,[4] the Siphonocladiales included all Chlorophyceae with multinucleate cells capable of dividing vegetatively. Many[5] still follow this interpretation of the order. However, such an interpretation overlooks the fact that it is a grouping of two families (Cladophoraceae and Sphaeropleaceae) that are related to the Ulotrichales[6] with two (Valoniaceae and Dasycladaceae) whose phylogenetic relationships seem to be with the Siphonales. One solution of this problem is seen[7] in the recent distribution of the various families to other orders. A more logical solution seems to be that of restricting the order to the two families evidently related to the Siphonales.

FAMILY 1. VALONIACEAE

The Valoniaceae have a plant body in which all cells except the rhizoids are more or less similar in form. Reproduction may be by fragmentation of vegetative portions or by means of biflagellate swarmers. Sometimes the zooids germinate directly; sometimes they unite in pairs.

There are about 15 genera and 90 species, all of them marine.

Valonia, a genus with about 15 species, is found in tropical and subtropical seas and in the Mediterranean. A half-dozen species are known[8] from Florida and the West Indies, and two are common algae of those regions. A young plant consists of a bladder-like primary cell which is attached to the substratum by unicellular rhizoids. The rhizoids are produced by an elongation of small lens-shaped cells cut off at the base of the primary cell (Fig. 64*D*). In *V. ventricosa* J.G.Ag., extensively studied by cellular physiologists, the primary cell always remains

[1] Just, 1882; Tobler, 1917. [2] Just, 1882; Maire, 1908; Tobler, 1917.
[3] Tobler, 1917. [4] Blackman and Tansley, 1902.
[5] Børgesen, 1913; Oltmanns, 1922; Printz, 1927; Taylor, 1928.
[6] Fritsch, 1935; Smith, G. M., 1933; West and Fritsch, 1927. [7] Fritsch, 1935.
[8] Taylor, 1928.

unbranched and may become 3 or more cm. in diameter. Primary cells of most other species cut off small lens-shaped daughter cells at the upper end, which grow to approximately the same size and shape as the primary cell (Fig. 64*A*, *C*). The resultant mass of more or less club-shaped cells may lie in a palisade-like cushion over 20 cm. broad.

A mature cell has a conspicuous central vacuole and a relatively thick layer of protoplasm external to the vacuole. Many angular chloroplasts

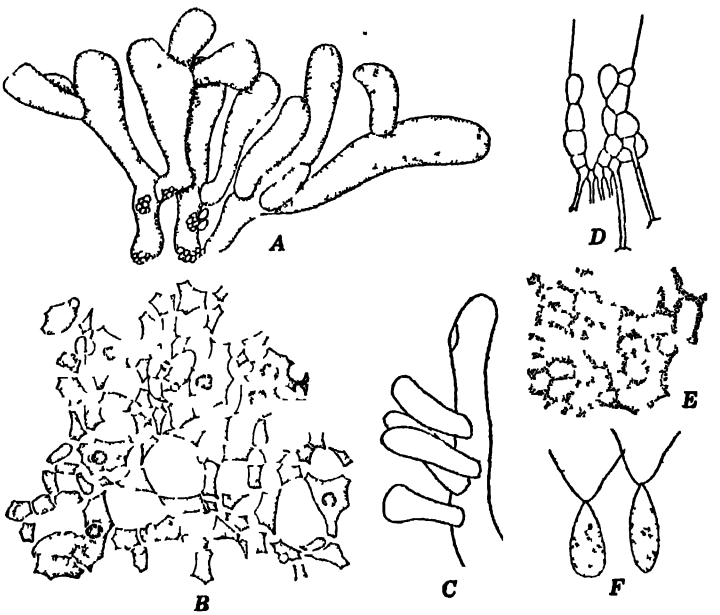


FIG. 64.—*A*, thallus of *Valonia utricularis* (Roth) C. A. Ag. *B*, chloroplasts and nuclei of *V. macrophysa* Kutz. *C*, lens cells of *V. utricularis*. *D*, rhizoids of *Aegagropila* C. A. Ag. *E*, reticulum of zooids in a cell of *V. macrophysa*. *F*, zooids of *V. macrophysa*. (*A–E*, *after Kuckuck*, 1907, *F*, *after Famintzin*, 1860.) (*A*, *C*, × 2, *B* × 600, *D–E*, × 12.)

lie embedded in the periphery of the cytoplasm,[1] where they have a tendency to form a reticulate arrangement with respect to one another (Fig. 64*B*). Most of the larger chloroplasts contain a single pyrenoid. The nuclei are somewhat larger than the chloroplasts and lie internal to them.

Any cell of a thallus may have its entire protoplast dividing into zooids. Species of *Valonia* growing in waters about Bermuda[2] produce zooids only during the summer months. Production of zooids has not been observed among undisturbed plants growing in the ocean. Plants brought into the laboratory and placed in aquariums sometimes produce zooids in abundance. The reticulate arrangement of the chloroplasts

[1] Kuckuck, 1907.

[2] I am indebted to my colleague Prof. L. R. Blinks for unpublished data concerning the Valonias of Bermuda

becomes more pronounced shortly before reproduction,[1] and, when the zooids are formed, they lie in a reticulum just within the cell wall (Fig. 64*E*). The zooids[2] are pyriform, biflagellate, uninucleate, and with two or three chloroplasts (Fig. 64*F*). Quadriflagellate zooids have been reported[3] for *V. macrophysa* Kutz., but in Bermuda this species forms biflagellate zooids. The zooids escape through pores developed in the upper side of the cell wall. Fertile cells of *V. macrophysa* may form[3] twenty or more pores through which the zooids escape singly. The zooids are generally liberated early in the morning.

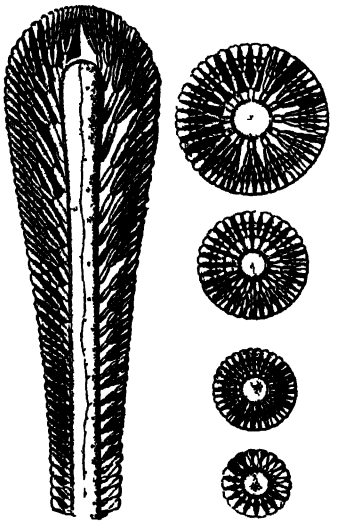


FIG. 65.—Reconstruction of *Palaeodasycladus mediterraneus* Pia. (*From Pia*, 1920) (× 8.)

Recent cytological studies of *V. utricularis* (Roth) C.A.Ag. indicate that there may be a gametic union of zooids. Certain individuals of this species have been shown[2] to have a reductional division of their nuclei just before formation of zooids. Gametic union of these zooids has not been observed, but stages of young zygotes have been found showing two gamete nuclei and a fusion of them into a single nucleus. Other individuals of *V. utricularis* do not have reductional divisions prior to a formation of zooids. It is thought that they produce zooids which germinate directly into new plants.

FAMILY 2. DASYCLADACEAE

Thalli of Dasycladaceae have a central axis bearing transverse whorls of branches from top to bottom or only at the upper end. All whorls of branches may be fertile, or some whorls may be fertile and others sterile. The protoplast of a fertile branch may divide directly into biflagellate isogametes, or it may form one or more aplanospores which produce biflagellate isogametes upon germination.

There are about 10 genera and 30 species, all marine and limited to warm waters.

Thalli of many genera are heavily encrusted with lime. Calcareous impressions or casts of these encrusted species may remain after death and decay of the plant body. Many such impressions and casts have been found in limestone rocks, and the geological record of these fossil

[1] Famintzin, 1860; Kuckuck, 1907. [2] Schechner-Fries, 1934.
[3] Kuckuck, 1907

Dasycladaceae extends back to the Ordovician.[1] The distinctive arrangement of lateral appendages in these fossil algae, often called *Siphoneae verticillatae*, shows that they are Dasycladaceae. There are about 45 genera of fossil Dasycladaceae.[1] Genera from the Carboniferous and earlier periods have their appendages irregularly distributed along the central axis. Those with whorled (verticillate) appendages (Fig. 65) are known from the Triassic onward.

Acetabularia, the mermaid's wineglass (Fig. 66*A*), is a genus with some 15 species. The two best known, *A. mediterranea* Lamx. and

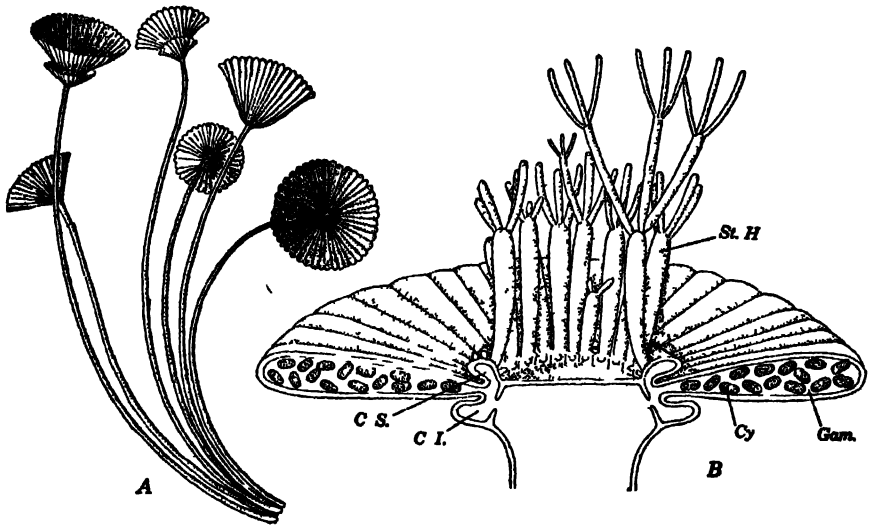


FIG 66.—*A*, thallus of *Acetabularia crenulata* Lamx. *B*, diagram of a vertical section of *A. mediterranea* Lamx. (*Based upon Oltmanns*, 1922.) *C I*, corona inferior; *C.S.*, corona superior; *Cy*, cysts, *Gam*, gametangium, *St. H.*, sterile hairs. (*A*, × 1½, *B*, × 8.)

A. Wettsteinii Schussnig, are found in the Mediterranean. Four species are found in Florida and the West Indies.[2] The mature thallus of *A. mediterranea* has an unbranched axis, 6 to 9 cm. tall, that terminates in an umbrella-like fertile cap about 1 cm. in diameter. The cap is strongly calcified and radially divided into a number of chambers. The thallus is perennial and does not fruit until it is three or four years old.

Gametic union takes place in the spring,[3] after which there is an immediate germination of the zygote into a sparingly branched *Vaucheria*-like filament (Fig. 67*D–F*). One of the branches is rhizoidal and penetrates the rock upon which the plant is growing. The rhizoid is colorless, irregularly lobed, and densely packed with starch. In the autumn[4] there

[1] Pia, 1927.

[2] Certain American phycologists (Howe, 1901; Taylor, 1928) list them as species of *Acetabulum* since they think this generic name has priority over *Acetabularia*.

[3] Hämmerling, 1934. [4] DeBary and Strasburger, 1877.

is a disintegration of the free-living portion after a cross wall has been formed between it and the embedded rhizoid (Fig. 67*G*). The persisting rhizoid sends forth a new upright axis the following spring and this axis bears one or more whorls of sterile branches at its apex (Fig. 67*H*). This axis disintegrates in the autumn, and the greatly enlarged rhizoid sends forth a new axis in the spring of the third year. The third-year axis may develop fertile branches after it has produced an apical whorl of sterile branches. The thallus is uninucleate throughout the entire period of vegetative development,[1] the nucleus being in one of the rhizoidal lobes. The nucleus is many-lobed, and. shortly before the

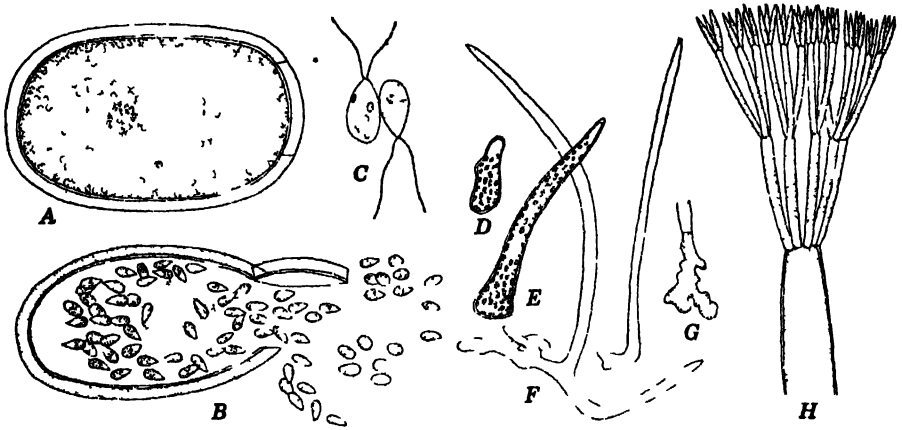


FIG. 67.—*Acetabularia mediterranea* Lamx. *A*, resting cyst. *B* germinating cyst. *C*, gametic union. *D–F* stages in early development of thallus. *G* overwintering rhizoid of first year. *H* apex of sterile (second year?) axis. (*After DeBary and Strasburger*, 1877.) (*A–B*, *D–E*, × 190, *C*, × 300, *F*, × 25, *G*, × 20, *H* × 48.)

formation of fertile branches, it divides into many small nuclei that move up the axis and into the developing fertile branches. The fertile branches are laterally apposed to one another in an umbrella-like disk (Fig. 66*B*). Each fertile branch bears a small basal lobe on its upper surface. The lobes are laterally fused with one another and jointly constitute the *corona superior*[2] *A. mediterranea* has a similar *corona inferior* on the under side of the fertile branches, but *A. Wettsteinii* lacks[3] a corona inferior. Sterile branches terminating the axis disappear as the fertile disk matures, and both the disk and upper portion of the axis may or may not become heavily calcified.

The protoplast of each fertile branch (a segment of the fertile disk) divides to form a number of aplanospores.[4] The aplanospores are uninucleate when first formed, later they become multinucleate.[4] Division of the primary nucleus of an aplanospore is reductional.[5]

[1] Hammerling, 1931. [2] Solms-Laubach, 1894. [3] Schussnig, 1930*C*.
[4] DeBary and Strasburger, 1877; Woronin, 1862; Schussnig, 1930*C*.
[5] Schussnig, 1929*A*.

Aplanospores are formed during the summer months but principally in July.[1] Aplanospores of *A. mediterranea* are strongly calcified and do not germinate (Fig. 67*B*) until the following spring; those of *A. Wettsteinii* are faintly calcified and may germinate a few days after they are formed.[1] The protoplast of an aplanospore divides to form many biflagellate gametes (Fig. 67*C*), each with several chloroplasts.[2] Liberation of gametes from aplanospores of *A. mediterranea* is due to a lid-like opening at one pole of the ellipsoidal aplanospore wall (Fig. 67*B*). Gametes from a cyst will not fuse with each other. However, there may be a fusion between gametes from two cysts produced upon the same plant.[1]

CLASS 2. CHAROPHYCEAE

The Charophyceae or stoneworts have an erect branched thallus differentiated into a regular succession of nodes and internodes. Each node bears a whorl of branches of limited growth—the "leaves." Branches capable of unlimited growth may arise axillary to the leaves. Sexual reproduction of Charophyceae is oögamous. The oögonia are one-celled, solitary, and surrounded by a sheath of spirally arranged sterile cells. The antheridia are one-celled, are united in uniseriate filaments, and have several filaments surrounded by a common spherical envelope composed of eight cells.

There are 6 genera and about 215 species. These constitute a very natural order, the *Charales*, with but one family, the *Characeae*.

The stoneworts are universally recognized as related to green plants, but there is great diversity of opinion concerning the degree of relationship. They have been considered an order of the Chlorophyceae, a class coordinate with the Chlorophyceae, and a division intermediate between algae and bryophytes. The vegetative structure and the sterile sheath about the sex organs are such distinctive features that the placing of them as an order of the Chlorophyceae seems too conservative a treatment. On the other hand, they cannot be considered a group standing at the bryophytic level because their sex organs are one-celled. The best solution of the problem seems to be that of interpreting them as an offshoot from the Chlorophyceae, but a series so far removed that it should be placed in a separate class.

Most of the Charophyceae grow submerged in fresh standing water and upon a muddy or a sandy bottom. When growing in ponds or lakes, they frequently form extensive subaquatic meadows that extend downward to a considerable depth below the surface of the water. They thrive best in clear hard waters, but a well-aerated water is not essential. Many species, especially those of *Chara*, become encrusted with calcium

[1] Hämmerling, 1934. [2] DeBary and Strasburger, 1877; Schussning, 1930*C*.

carbonate, and the continued presence of the alga from year to year may result in the deposition of considerable calcareous material upon the lake bottom. The calcareous deposit about the plant may remain intact after decay of the organic material, and several fossil Charales have been described from such calcareous casts. The structure of the fruit of Charales, especially that of the female fructification, is so distinctive that the systematic position of the plants producing these casts is fairly

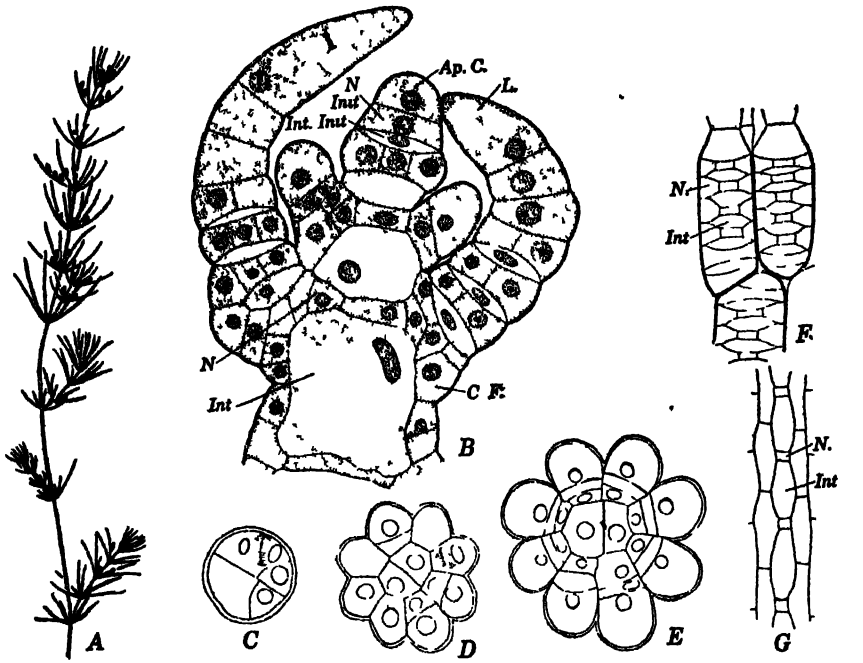


FIG. 68.—*Chara* sp. *A*, thallus *B*, vertical section of thallus apex. *C–E*, transverse sections of second, third, and fourth nodes *F*, young corticating branches. *G*, portion of a mature corticating branch (*Ap C.*, apical cell, *C F*, corticating filament, *Int*, internode, *Int Init*, internodal initial, *L*, leaf, *N*, node, *N. Init*, nodal initial) (*A*, × ⅔, *B*, × 210; *C F*, × 145, *G*, × 105)

certain. Fruits of fossil Charophyceae have been found as far back as the Palaeozoic.[1] Fossil remains of *Chara*-like vegetative tissues are known from as early as the Upper Devonian,[2] but the systematic position of these plants is not so certain.

Chara is a widely distributed genus with about 90 species. These can only be distinguished from one another when in a fruiting condition. The thallus is an erect branched axis that is attached to the substratum by rhizoids. The rhizoids are uniseriate branched filaments with or without a differentiation into nodes and internodes. The erect axis has an *Equisetum*-like differentiation into nodes and internodes (Fig. 68*A*). Each node bears a whorl of several branches (the leaves) that

[1] Pia, 1927. [2] Kidston and Lang, 1921.

cease to grow after they have formed three to eight nodes and internodes. A node may also bear one or more branches in which growth may continue indefinitely. In a few species the internode consists of a single cell many times longer than broad. In a majority of species this internodal cell is ensheathed (corticated) by a layer of vertically elongate cells of much smaller diameter. The ensheathing layer (the *cortex*) is always one cell in thickness.

Terminal growth of an axis and its branches is initiated by a single dome-shaped apical cell which cuts off derivatives at its posterior face (Fig. 68*B*). A derivative cut off by an apical cell soon develops into a node and its underlying internode. Each derivative divides transversely. The inferior daughter cell remains undivided, elongates to many times its original length, and matures into an internodal cell. The superior daughter cell (the *nodal initial*) divides and redivides to form the node and the corticating tissue of species in which the internodes are corticated. The first division of a nodal initial is vertical, and the two daughter cells also divide vertically and in a plane intersecting the first plane of division.[1] Succeeding divisions are also vertical and in a plane intersecting the preceding plane of division. The nodal tissue produced by these divisions consists of two central cells and an encircling ring of 6 to 20 peripheral cells. The central cells may remain undivided, or they may divide two or three times (Fig. 68*C–E*). All of the peripheral cells divide periclinally. The inner daughter cells produced by periclinal division may remain undivided or divide vertically. The outer daughter cells function as apical cells and give rise to the leaves.

The apical cell of a "leaf" cuts off derivatives in the same manner as the apical cell of a main axis. The first derivative develops into the basal node of a leaf. All other derivatives eventually produce a node and an underlying internode. The apical cell of a leaf becomes conical and ceases division after it has cut off 5 to 15 derivatives. Internodal cells of leaves develop in the same manner as those of an axis except that they do not become as long. Nodes of leaves develop in much the same sequence as those of an axis. They have but one central cell, and the peripheral cells never become apical cells. Instead, all or certain of the embryonic peripheral cells mature into one-celled spine-like appendages—the "*stipules*."

Half of the corticating tissue of an internode of an axis is derived from the node above, and the other half is derived from the node below. The basal node of each leaf produces a single ascending *corticating initial* and a single descending one. Each corticating initial is an apical cell which gives rise to a *corticating branch* that lies closely applied to the internodal cell. Collectively the corticating branches between two nodes constitute the

[1] Giesenhagen, 1896, 1897, 1898.

corticating tissue (cortex) of the intervening node. A corticating branch is differentiated into three-celled nodes and one-celled internodes (Fig. 68*F*). All cells of embryonic corticating branches are approximately the same length, but the two lateral nodal cells and the internodal cell eventually elongate to many times their original length (Fig. 68*G*). The median cell of a node does not elongate. These cells may or may not develop stipules. Cortication of a leaf may be similar to that of an axis, or the corticating initials at the leaf nodes may elongate without dividing.

Cells near a branch apex are without conspicuous vacuoles and are always uninucleate. Greatly enlarged cells of mature regions, as those of an internode and of the stipules, have a large central vacuole. The layer of cytoplasm between cell wall and central vacuole contains many small ellipsoidal chloroplasts and a few large irregularly shaped nuclei. The nuclei increase in number by constriction (*amitosis*). The chloroplasts lie in parallel, longitudinal, spirally twisted files. The cytoplasm next to the central vacuole revolves continuously in a longitudinal direction, and there is an ascending stream of cytoplasm on one side of a cell and a descending stream on the other. The upward and downward streams are laterally separated from each other by a motionless streak of cytoplasm without chloroplasts.

None of the Charales produces zoospores, but several of them produce vegetative propagative bodies. Vegetative propagation may be effected by: (1) star-shaped aggregates of cells developed about the lower nodes (frequently called *amylum stars* because they are densely filled with starch); (2) *bulbils* developed upon the rhizoids, and (3) protonema-like outgrowths from a node.

All species of *Chara* reproduce sexually. The male and female fructifications are generally called antheridia and oögonia, but these names are inappropriate because the structures so designated include both the sex organ (or organs) and an enveloping multicellular sheath. According to the old terminology[1] the male fructification is a *globule* and the female is a *nucule*. These names are more appropriate since they do not imply that the entire fructification is the sex organ. Globules and nucules are always borne at the nodes of leaves and on the side facing the axis. A few species are heterothallic. Most of them are homothallic and have a globule and a nucule at each fertile node. The two fructifications always have a definite orientation with respect to each other, and the nucule always lies above the globule (Fig. 70*A*). The two may develop simultaneously, or development of the globule may be somewhat in advance of that of the nucule.

[1] Sachs, 1875.

A superficial nodal cell on the adaxial side of a fertile leaf functions as an apical cell that cuts off two derivatives The lower derivative divides and redivides to form a node The upper derivative enlarges to form an internodal cell that becomes the *pedicel cell* of the future globule (Fig 69*A*) The apical cell becomes spherical and divides vertically[1] to form four quadrately arranged cells, each of which divides transversely (Fig 69*B*) Each octad divides periclinally, and the eight outer daughter cells also divide periclinally (Fig 69*C*) The outer of the three cells derived from each octad is a *shield cell*, the median is a

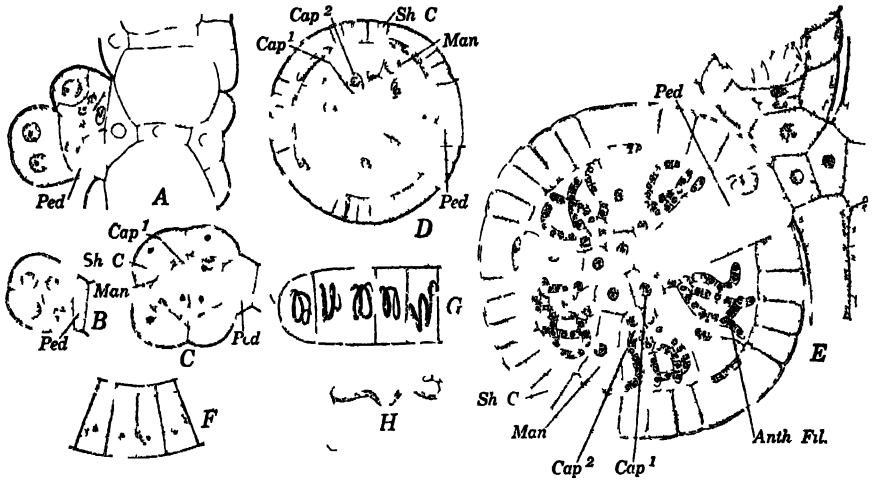


FIG 69 *A F* development of gl ule of *Cha a* sp *F H Chara fœtida* A Br *F–G* antheridial filaments *H*, anther zoid (1 *th Fil* antheridial filament (*ap* 1, primary capitulum (*ap* 2 secondary capitulum *Man* manubrium *P d* pedicel *Sh C* shield cell) (*I H* Ift r *Bel g* 1894) (1 C × 210 *D E* × 145 *F G* × 575 *H* × 290)

handle cell or *manubrium* and the inner is a *primary capitulum* Maturing shield cells expand laterally, and a cavity develops within the globule The manubria elongate radially as the cavity develops, but the primary capitula continue to lie apposed to one another There is also an upgrowth of the pedicel cell into the cavity within the globule The outer periclinal wall of a maturing shield cell develops radial ingrowths which incompletely divide the cell into a number of compartments Hence the outer layer of a maturing globule seems to be many cells in perimeter when it is viewed in cross section. Mature globule are a bright yellow or red because of a change in color of chloroplasts within the shield cells.

Each primary capitulum within a globule cuts off six *secondary capitula* (Fig 69*D*), and these may or may not cut off tertiary and quaternary capitula[2] The capitular cells then cut off initials of *antheridial filaments* These initials are usually cut off from secondary

[1] Campbell, 1902; Sachs, 1875 [2] Karling, 1927

capitula, but they may be produced upon primary, tertiary, or quaternary ones. The antheridial filaments developed from antheridial initials may be branched or unbranched (Fig. 69*E*). The number of cells in a filament varies greatly, and, even in the same species, it may range from 5 to 150.[1] Each cell of a fully developed filament is an *antheridium*, and its protoplast metamorphoses into a single *antherozoid*. The nucleus of a metamorphosing protoplast (Fig. 69*F–G*) moves toward the side wall, elongates, and becomes spirally coiled.[2] Meanwhile, there has been a differentiation of a spirally coiled *blepharoplast* (the flagellum-forming body) just within the plasma membrane. Two long flagella are formed, and they are attached a short distance back from the anterior end of the coiled antherozoid (Fig. 69*H*). When the antherozoids are mature, the shield cells of a globule separate from one another, freely exposing the antheridial filaments attached to the capitula upon the manubria. The manubrium, with its attached capitula and antheridial filaments, resembles a many-thonged whip. The antherozoids then escape through a pore in the antheridial wall. Liberation of antherozoids generally takes place in the morning,[3] and the swarming may continue until evening.

The globule has been interpreted[4] as a metamorphosed branch in which the terminal cell divides into octants. The octants are considered lateral appendages. Each of them is differentiated into a basal node (the shield cell), an internodal cell (the manubrium), and an upper nodal cell (the primary capitulum). The filamentous outgrowths (antheridial filaments) from the upper node are not differentiated into nodes and internodes.

An adaxial cell of the basal node of a globule functions as the initial of a nucule. This initial divides transversely to form a row of three cells.[5] The uppermost and lowermost of these are internodal in nature, and the median is nodal. The lower internodal cell remains undivided and enlarges to form the *pedicel cell* subtending the nucule (Fig. 70*B*). The upper nodal cell is an *oogonial mother cell* which elongates vertically and then divides transversely to form a short *stalk cell* and a vertically elongate *oogonium* (Fig. 70*C*). The oögonium contains a single uninucleate *egg* whose protoplast becomes packed with large starch grains before fertilization. Even before elongation of the oögonial mother cell, there is a vertical division and redivision of the nodal cell to form five lateral initials encircling a single central cell. The five lateral initials grow upward to form a protective sheath enclosing the oögonial mother cell (Fig. 70*C*). The sheath soon becomes transversely divided into two tiers of five cells each (Fig. 70*D*). Cells of the upper tier elongate but

[1] Karling, 1927. [2] Belajeff, 1894; Mottier, 1904. [3] Sachs, 1875.
[4] Goebel, 1930. [5] Campbell, 1902; Debski, 1898; Goetz, 1899; Sachs, 1875.

little and mature into the five-celled *corona* capping a mature nucule. Those of the lower tier, the *tube cells*, elongate to many times their original length and become spirally twisted about the oögonium (Fig. 70*E–F*).

The spirally twisted tube cells of a mature sheath separate from one another just below the corona to make five small angulate slits.[1] Antherozoids swim through these openings in the sheath of a nucule and

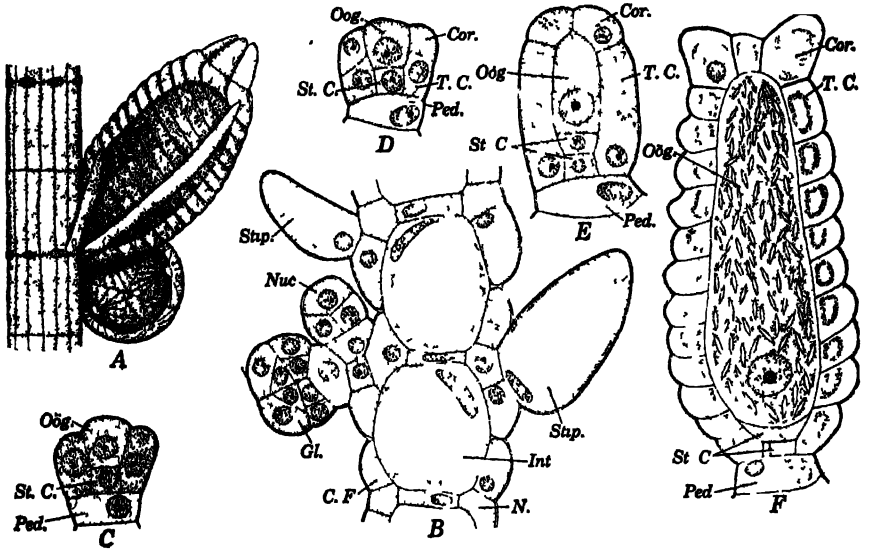


FIG. 70.—*Chara* sp. *A*, portion of a leaf bearing a mature globule and nucule. *B*, vertical section of a leaf bearing a very young globule and nucule. *C–F*, stages in development of a nucule. (*Cor.*, corona; *C F*, corticating filament, *Gl*, globule, *Int.*, internode; *N*, node; *Nuc.*, nucule; *Oög.*, oogonium; *Ped*, pedicel; *St C.*, stalk cell, *Stip.*, stipule; *T. C.*, tube cell.) (*A*, × 50; *B–E*, × 210; *F*, × 145.)

down to the oögonium (Fig. 71*A*). One of them penetrates the gelatinized oögonial wall and unites with the egg. Male gamete nuclei have been observed within eggs of another genus (*Nitella*),[2] and it is thought that there is the same union of gamete nuclei at the base of the egg, in *Chara*.

The zygote secretes a thick wall, and the inner tangential walls of the tube cells also thicken. Other walls of the sheath decay, leaving the hardened inner walls projecting from the zygote like the threads on a screw. The zygote, with surrounding remains of the sheath, falls to the bottom of the pool and there germinates after resting for a few weeks or more. The zygote nucleus migrates to the apical pole of the zygote and there divides[3] into four daughter nuclei (Fig. 71*B*). This division into four nuclei suggests that division is reductional. Confirmatory evidence for this supposition is found in the absence of meiosis prior to the forma-

[1] DeBary, 1871. [2] Goetz, 1899. [3] Oehlkers, 1916.

tion of gametes.[1] According to such an interpretation, the thallus is a gametophyte, and the zygote is the only diploid cell in the life cycle

Germination begins with an asymmetrical division of the quadrinucleate zygote into a small lenticular distal cell with one nucleus, and a large basal cell containing the other three nuclei (Fig. 71*C*). The lentic-

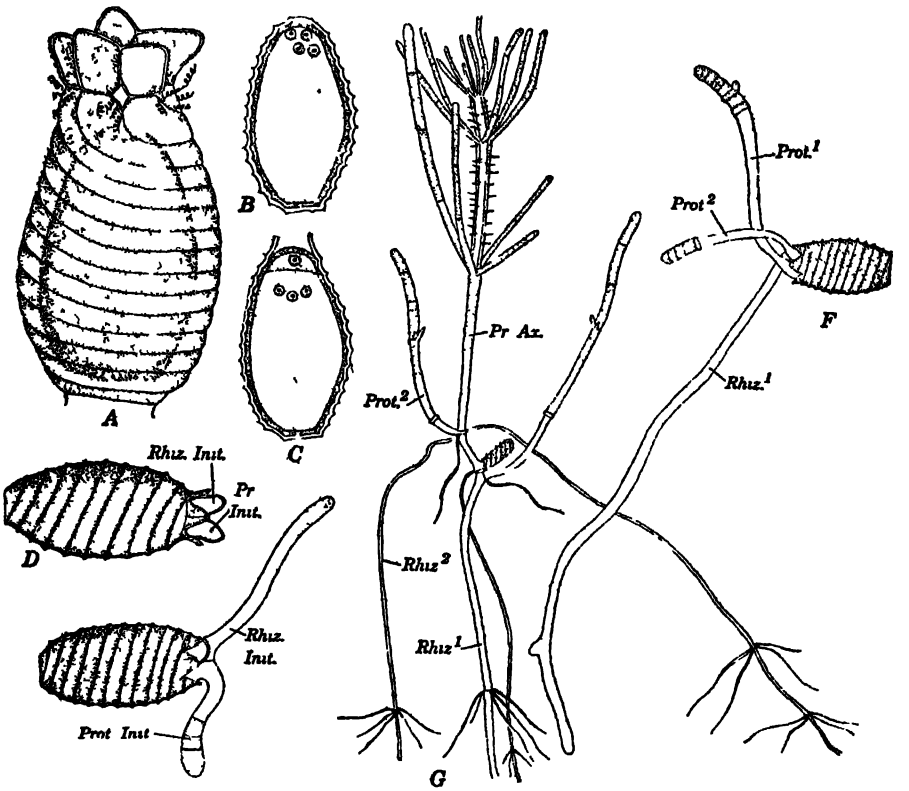


FIG. 71.—*A C*, *Chara foetida* A Br *D G*, *C crinata* Wallr *A*, entrance of antherozoids into nucule *B–C*, diagram of longitudinal sections of germinating zygotes. *D–E*, surface views of germinating zygotes *F*, germling at protonematal stage *G*, young plant after development of first nodal branches (*Pr Ax*, primary axis, *Prot* [1], primary protonema, *Prot* [2], secondary protonema, *Prot Init*, protonematal initial, *Rhiz* [1], primary rhizoid, *Rhiz* [2], secondary rhizoid *Rhiz Init*, rhizoidal initial) (*A*, *after DeBary*, 1871, *B–C*, *based upon DeBary*, 1875 *and Oehlkers*, 1916, *D–F*, *after DeBary*, 1875) (*A*, × 70; *B–C*, × 45, *D–E*, × 50, *F*, × 25, *G*, × 4)

ular cell soon becomes exposed by a cracking open of the zygote wall. This cell then divides vertically into a *rhizoidal initial* and a *protonematal initial* (Fig. 71*D–E*). The large three-nucleate cell remains undivided, and its nuclei eventually disintegrate. The rhizoidal initial develops into a colorless rhizoid,[2] differentiated into nodes and internodes, and one with a whorl of secondary rhizoids growing out at each node. The

[1] Lindenbein, 1927 [2] DeBary, 1875.

protonematal initial develops into a green filament (the *primary protonema*), also differentiated into nodes and internodes (Fig. 71*F*). Appendages produced by the lowermost node of a primary protonema mature into rhizoids or into secondary protonemata. The second node of a primary protonema bears a whorl of appendages (Fig. 71*G*). All but one of them are simple green filaments. The remaining appendage develops into a typical axis in which growth is as in an adult plant.

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CHAPTER III

EUGLENOPHYTA

The Euglenophyta have colorless protoplasts or protoplasts with their pigments localized in grass-green chloroplasts. Irrespective of whether nutrition is holophytic, saphrophytic, or holozoic, the food reserves are either *paramylum* (an insoluble carbohydrate related to starch) or fats. Almost all members of the division are naked unicellular flagellates, either with a rigid protoplast or with one that is constantly changing in shape. Motile cells may have one, two, or three flagella. These are inserted at the anterior end of a cell and almost always at the base of an interior chamber connected with the exterior of the cell by a narrow gullet. Reproduction is generally by cell division. Thick-walled resting stages (cysts) are known for several genera. Sexual reproduction is of extremely rare occurrence and seems definitely established for one genus only.

There are about 25 genera and 335 species, almost all of which are fresh-water.

The euglenoids are a sharply defined series of colorless and pigmented organisms that have more in common with the Protozoa than do other series of pigmented protista. Aside from the fact that they may have chromatophores and a plant-like mode of nutrition, the chief justification for including them in the plant kingdom is the fact that one genus (*Colacium*) has a truly algal organization in which immobile palmelloid cells are the dominant phase in the life cycle.

The relationships between Euglenophyta and other algal series are obscure. Similarities in pigmentation and food reserves of Euglenophyta and Chlorophyta tempt one to make them a class (Euglenophyceae) of the Chlorophyta. However, the organization of the protoplast is so different from that of Chlorophyta that it is better to follow the usual practice and accord the euglenoid series a rank equal to that of the chrysophycean, dinoflagellate, and volvocine (chlorophycean) series.

The first formal recognition of the euglenoids as a division (Euglenophyta) of the plant kingdom[1] divides them into two classes, each with a single order. A more logical treatment seems to be that of placing them in a single class, the Euglenophyceae, because differences between the two orders are of the same magnitude as in orders of Chlorophyceae, Chrysophyceae, and other classes of algae.

[1] Pascher, 1931.

ORDER 1. EUGLENALES

The Euglenales include all of the Euglenophyceae in which the flagellated motile cell is the dominant phase in the life cycle.

All but one of the genera of Euglenophyta belong to this order. Most of the genera are found in fresh waters, and chiefly in small pools rich in organic matter. Pigmented forms, especially *Euglena*, are frequently present in sufficient abundance to color the water. The colorless forms are rarely found in quantity, but sometimes they are fairly numerous in waters containing decaying organic matter.

Cell Shape. Motile euglenoids are always solitary and never in temporary or permanent colonies (Fig. 72). The exterior portion of the cytoplasm is always differentiated into a periplast. This may be so rigid that the cells have a fixed shape, or it may be so flexible that the shape of the cell is constantly changing as it swims through the water. Cells with a flexible periplast are more or less elongated and approximately circular in transverse section. Those with a firm periplast may be radially symmetrical or markedly compressed.

Species with a firm periplast frequently have one that is longitudinally or spirally ridged or striate. Three genera have the protoplast surrounded by an envelope (*lorica*) that stands free from the protoplast (Fig. 72*B–C*). The lorica is always open at the anterior end and has the flagella projecting through the opening. A lorica is composed of a firm gelatinous substance without any trace of cellulose.[1] It is colorless and transparent when first formed; later it frequently becomes impregnated with iron compounds, opaque, and yellow to dark brown in color. The shape and ornamentation of the lorica are characteristic for any given species and are the chief characters in differentiating species within genera having loricae.

Cell Structure. Cells of many euglenoids contain chloroplasts. There are usually several of them in a cell, and they may be discoid, band-shaped, or stellate. The chloroplasts are always a bright green. In a few species, as *Euglena sanguinea* Ehr., the cells may also produce a red pigment (haematochrome), which may be produced in such quantities as to obscure the cell contents. Results of spectroscopic analyses of the green pigments are contradictory since it has been affirmed[2] and denied[3] that their absorption curve closely approximates that of the green plants. Many of the species with chloroplasts have one or more conspicuous pyrenoids, either within or without the chloroplasts. Pyrenoids contained within chloroplasts may possibly be concerned with the formation of reserve foods, but those external to chloroplasts seem to have no connection with reserve-food formation.[3]

[1] Klebs, 1883. [2] Baas-Becking and Ross, 1925. [3] Günther, 1928.

The chief product of photosynthesis is *paramylum*, a carbohydrate with the same empirical formula as starch, but one that does not respond[1] to the usual tests for starch. Cells with chloroplasts may also form paramylum as a result of an osmotic intake of dissolved foods from the surrounding water or as a result of an ingestion of solid foods.[2] The nutrition of colorless species is always saphrophytic or holozoic. Ingestion of solid food takes place through the *cytostome*, a differentiated softer portion of the periplast. The gullet at the anterior end of a cell functions as the cytostome of most Euglenales, but there are species[3] with a cytostome distinct from the gullet. Paramylum is always formed in the cyto-

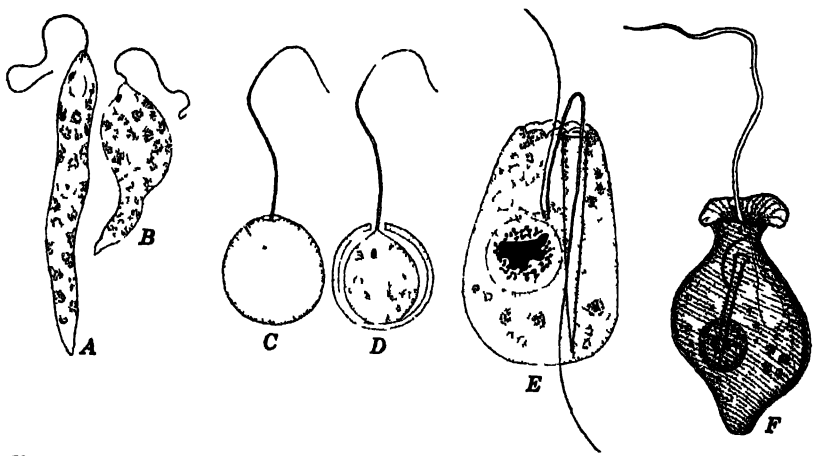


FIG. 72.—Euglenales. *A–B*, *Euglena intermedia* (Klebs) Schmitz; *C*, *D*, surface view and optical section of *Trachelomonas volvocina* Ehr., *E*, diagrammatic ventral view of *Entosiphon sulcatum* (Duj.) Stein *F*, *Urceolus cyclostomus* (Stein) Mereschk (*E*, *based upon Lackey*, 1929, *F*, *after Senn*, 1900.) (*A–B*, × 325; *C–D*, × 650; *F*, × 1,000.)

plasm. It is laid down in spherical, discoid, bacillar, or annular granules that sometimes become relatively large. Paramylum granules resemble starch grains in that they appear to be concentrically stratified. However, the apparent concentric stratification has been held[4] to be due to a helical twisting of elongate threads of paramylum rather than to a deposition of paramylum in concentric lamellae. Reserve foods of Euglenales may also be stored in the form of minute droplets of oil.

The nucleus of the euglenoid cell is a prominent structure and one easily recognized without staining. All Euglenales are uninucleate under normal conditions, but a cell may become multinucleate if cytokinesis is inhibited.[5] The nucleus has a conspicuous karyosome, a well-defined membrane, and considerable chromatic material between the

[1] Bütschli, 1906; Haye, 1930; Klebs, 1883. [2] Mainx, 1928*A*; Tannreuther, 1923.
[3] Brown, 1930. [4] Heidt, 1937. [5] Mainx, 1928.

two. Resting nuclei lie near the center of a cell, but those about to divide may move toward the anterior end of a cell. The chromatic material of a dividing nucleus becomes organized into a definite number of chromosomes that lie with their long axes perpendicular to the plane of nuclear division (Fig. 73). The mitotic separation of chromosomes is accompanied by a bipartition of the karyosome. The nuclear membrane persists throughout all stages of mitosis.[1]

The gullet at the anterior end of a cell is usually flask-shaped and differentiated into a narrow neck, the *cytopharynx*, and an enlarged posterior portion, the *reservoir*. The reservoir, in turn, is adjoined by one or more contractile vacuoles in which the interval between cystole and diastole is usually but a few seconds.[2] Certain genera have *rod organs* (*pharyngeal rods*) adjacent to the gullet. There are usually two of them in a cell. They lie parallel with the long axis of the gullet and with their lower extremities level with the base of the reservoir or extending to the posterior portion of a cell (Fig. 72*E–F*). Some of the genera with rod organs seem[3] to have them terminating beneath a cytostome entirely distinct from the gullet. The function of the rod apparatus has been thought to be that of a trichite which serves as a supporting organ for the distended cytostome.[4]

Flagella of Euglenales are inserted in the base of the reservoir and project through the cytopharynx. Uniflagellate genera have the flagellum projecting forward. Some biflagellate genera have both flagella of equal length and projecting forward, but more genera have flagella of unequal length, one projecting forward and the other trailing. Euglenoid flagella are of the "feather" type, with a single row of diagonally inserted cilia along one side.[5] A majority of the genera investigated have been shown to have a neuromotor apparatus of the blepharoplast-rhizoplast-centriole type. Some of the uniflagellate genera have the flagellum bifurcating within the reservoir and each fork terminating in a blepharoplast. One of the blepharoplasts is connected with an extranuclear centriole by a delicate rhizoplast; the other is without a rhizoplast. Other uniflagellate genera do not have a bifucation of the flagellum, but they may have a granular swelling some distance above the blepharoplast (Fig. 73). Biflagellate genera do not have forking of either flagellum, but there may be granular swellings above the blepharoplasts. Both daughter nuclei are connected with a neuromotor apparatus shortly after mitosis is completed and before division into two daughter cells.[6] It has

[1] See Hall, 1923; Baker, 1926, and Lackey, 1934, for the literature on mitosis.
[2] Günther, 1928; Hall and Powell, 1928.
[3] Brown, 1930; Lackey, 1929; Rhodes, 1926.
[4] Hall and Powell, 1928; Rhodes, 1926; Schaeffer, 1918. [5] Petersen, 1929.
[6] Baker, 1926; Brown, 1930; Hall, 1923; Hall and Powell, 1927, 1928; Lackey, 1934.

been held[1] that both have been formed anew, but it is more probable that the neuromotor system attached to one daughter nucleus is that which was attached to the original nucleus and that the system of the other daughter nucleus has been formed *de novo*.[2]

Most of the Euglenales with chloroplasts and certain of the colorless species have an eyespot at the anterior end of a cell. It is a more or less flattened plate, and in certain cases it is held[3] that there is a hyaline lens external to the pigmented plate.

Asexual Reproduction. Multiplication is by cell division, and it may take place while the cells are actively motile or after they have come to rest. Cell division is longitudinal and begins at the anterior end of a cell (Fig. 73). In some species, cells come to rest before division, often developing a gelatinous sheath. Sometimes the daughter protoplasts do not

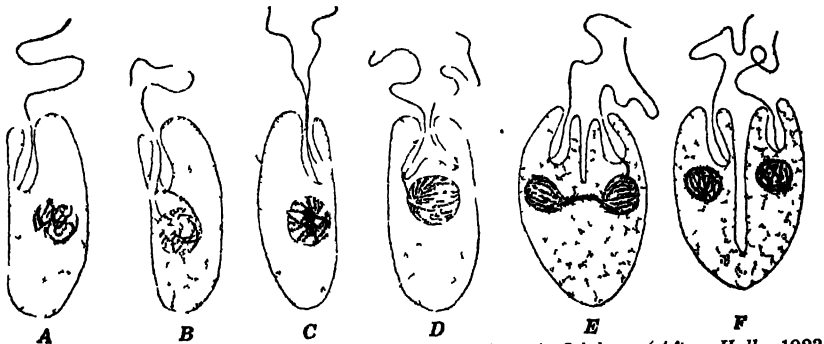


FIG. 73.—Cell division of *Monadium incurvum* (Ires.) Klebs (*After Hall*, 1923.) (× 1 400)

escape from the gelatinous matrix before they divide again.[4] In such cases there is a development of temporary palmelloid colonies in which the cells may return to a motile condition at any time. Genera with a lorica have the protoplast dividing within the lorica. One of the daughter protoplasts remains within the old lorica; the other escapes and secretes a new lorica.

Thick-walled resting stages (cysts) are common in many genera. Sometimes the cyst is of the same general shape as a motile cell, but more often it is quite different in shape and either spherical or polygonal. Protoplasts of cysts may produce a considerable amount of haematochrome and become a deep red. Germinating cysts usually have the protoplast escaping from the wall and developing into a single motile cell.

Sexual Reproduction. Gametic union has been described for a few euglenoids,[5] but the only well-authenticated case seems to be that of

[1] Baker, 1926. [2] Loefer, 1931. [3] Mast, 1928.
[4] Dangeard, 1901; Tannreuther, 1923
[5] Berlmer, 1909; Dobell, 1908; Haase, 1910.

Scytomonas (*Copromonas* Dobell). However, the only fact established with certainty is the fusion of motile gametes, since the supposed division of nuclei observed[1] in conjugating cells of *Scytomonas* is extremely doubtful.

Classification. Several systems[2] for the classification of Euglenales stress the mode of nutrition and group them in three families according to their holophytic, saphrophytic, or holozoic nutrition. Such a classification is arbitrary because there are certain genera, as *Euglena*, in which some species have chloroplasts and other lack them. The best basis for a differentiation into families seems to be the finer cytological structure, especially that of bifurcation and granulation of flagella.[3] The taxonomic significance of the pharyngeal rod apparatus is less certain. Some euglenophiles[4] place great emphasis on this structure; others[5] hold that it is one of minor importance. In any case, only three or four families are recognizable within the order.

ORDER 2. COLACIALES (EUGLENOCAPSALES)

The Colaciales have immobile cells permanently encapsulated within a wall and united in amorphous or dendroid palmelloid colonies. There may be a temporary formation of naked uniflagellate stages.

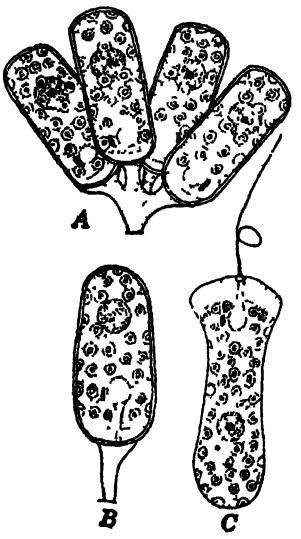


FIG. 74.—*Colacium calvum* Stein. (*After Stein*, 1878.)

The single genus, *Colacium*, is epizoic upon copepods, rotifers, and other members of the fresh-water zooplankton. There are but two species.

Cells of *Colacium* (Fig. 74) are surrounded by a gelatinous envelope and are affixed, with the anterior pole downward, by means of gelatinous stalks, to the host. The stalks are the result of a greater secretion of gelatinous material at the anterior end of a cell. When cell division takes place, each of the two daughter cells secretes a stalk of its own, and they remain attached to the stalk of the parent cell. Repeated cell division results in a dendroid colony in which the cells are borne at the extremities of a repeatedly branched gelatinous-stalk system.

The cells of dendroid colonies are ovoid or subcylindrical. They contain numerous discoid chloroplasts, with or without pyrenoids. There

[1] Dobell, 1908. [2] Klebs, 1892; Lemmermann, 1913; Senn, 1900.
[3] Hall and Jahn, 1929; Lackey, 1934. [4] Brown, 1930; Rhodes, 1926.
[5] Hall and Jahn, 1929.

is a single large nucleus toward the upper end of a protoplast. The lower portion of a protoplast, the morphologically anterior end, contains a conspicuous gullet and an eyespot. Flagella are not evident in protoplasts of dendroid colonies.[1]

Cells grown in culture on agar slants are globose and surrounded by an envelope that is without a stalk.[2] Their daughter cells may separate from each other immediately following cell division, or the two may remain within the parent-cell envelope. Repeated division of cells within a common envelope may continue until there is an amorphous palmelloid colony of 20 or more cells. Palmelloid cells are ordinarily uninucleate, but they may become larger than usual and two- to eight-nucleate.

Protoplasts of *Colacium* may also develop into naked amoeboid stages that divide vegetatively.[3] There may also be a formation of naked amoeboid stages with four to eight nuclei.[2] The only known method of reproduction in these plasmodial stages is a budding off of uninucleate portions and a metamorphosis of them into uniflagellate swarmers.

A cell of the dendroid or palmelloid stage may have its protoplast developing a single flagellum and escaping as a free-swimming zooid.[4] Such zooids (Fig. 74*C*) usually swarm for a short time only before they lose their flagella and secrete walls. In rare cases[5] a zooid may divide into two daughter zooids while in a motile condition.

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[1] Stein, 1878. [2] Johnson, 1934. [3] Schiller, 1924.
[4] Johnson, 1934; Stein, 1878. [5] Johnson, 1934; Schiller, 1924.

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CHAPTER IV

PYRROPHYTA

The Pyrrophyta have protoplasts with pigments localized in yellowish-green to golden-brown chromatophores. Photosynthetic reserves generally accumulate as starch or starch-like compounds, but they may also accumulate as oil. Cell walls, when present, generally contain cellulose. Most members of the division are unicellular biflagellate organisms with or without a definite wall. Some genera are without flagella, alga-like, and either unicellular or colonial. Immobile genera may reproduce by means of zoospores or aplanospores. Sexual reproduction is found in but two or three genera.

There are about 135 genera and 1,000 species; some marine, others fresh water.

The Pyrrophyta differ from other algae with more or less brownish chromatophores in that they form starch or starch-like compounds. For a long time all known genera were unicellular biflagellate organisms whose affinities were thought to be with the protozoa. During recent years a few truly algal unicellular and colonial forms have been discovered which obviously are related to the earlier known motile forms.

The Pyrrophyta have been divided[1] into three classes.

CLASS 1. CRYPTOPHYCEAE

Protoplasts of Cryptophyceae usually contain two more or less brownish chromatophores with or without pyrenoids. Reserve foods of a cell generally accumulate as starch or starch-like compounds. Motile cells are compressed and biflagellate, with the flagella slightly different in length and inserted either terminally or laterally.

There are about 12 genera and 30 species, most of which are fresh-water.

The Cryptophyceae are a small, imperfectly known, phyletic series in which most of the genera are motile unicellular *cryptomonads*, but in which two of the genera are immobile nonflagellated algae. The affinities of the cryptomonads were thought to be with the chrysomonads until Pascher[2] showed that they have more in common with the dinoflagellates. Later, he proposed[3] that the cryptomonads and dinoflagellates be placed in a separate division, the Pyrrophyta.

[1] Pascher, 1911, 1914, 1931. [2] Pascher, 1911. [3] Pascher, 1914, 1931.

Fresh-water cryptomonads usually grow in waters rich in organic and in nitrogenous material. They frequently grow in waters containing euglenoids, sometimes growing in considerable abundance.

The motile genera are placed in a single order, the Cryptomonadales. Their cells are compressed and have a superficial curved longitudinal furrow extending back from the point of insertion of the flagella (Fig. 75). Cryptomonads with terminally inserted flagella have a truncate anterior end and a broadly rounded posterior end. Those with laterally inserted flagella have more or less reniform cells Most cryptomonads have the surface near the insertion of flagella invaginated to form a gullet that extends deep into the protoplast (Fig. 76). The gullet is generally rigid and surrounded by a layer of colorless rod-like or granular *trichoblasts*. The function of the gullet is uncertain, and it is not definitely established that

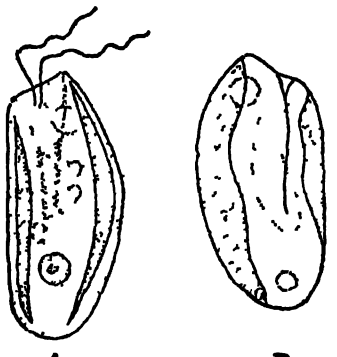


FIG. 75.—*Cryptomonas ovata* Ehr (*A*, *after Stein*, 1878, *B*, *after Pascher*, 1913)

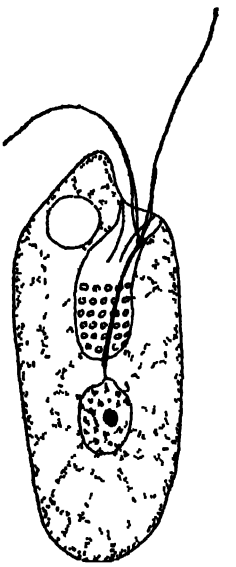


FIG 76.—*Chlomonas Paramaecum* Ehr (*After Ulehla*, 1911)

cryptomonads ingest solid foods[1] There is a single large contractile vacuole at one side of the gullet, and it seems to discharge its contents into the gullet.

The two flagella may be inserted in the gullet rather than on the free surface of a cell. One cryptomonad is known[1] to have a definite neuromotor apparatus with the blepharoplast connected to the nucleus by a conspicuous rhizoplast. Flagella of cryptomonads are slightly different in length and usually somewhat flattened. Both may project forward, or one may project forward and the other trail as a cell swims through the water.

[1] Ulehla, 1911.

Most species have two laminate chromatophores just within the plasma membrane and running longitudinally through a cell. Their color is generally an olive-green to a golden brown, but it may be blue-green or a Burgundy red. Pyrenoids of some species are embedded in the chromatophores; those of other species lie in the cytoplasm. In either case, the starch or starch-like granules of a cell may either encircle the pyrenoids or lie along the inner face of the chromatophores. Accumulation of starch and other reserve foods may be due either to photosynthetic activity or to a saprophytic nutrition of the cell.



A *B*

FIG. 77.—*Phacotlax marinus* (Reinsch) Pascher. *A*, vegetative colony, *B*, zoospore. (*After Reinsch*, 1911.) (*A*, × 1,000, *B*, × 1,500.)

Cryptomonads are uninucleate and with the nucleus toward the posterior end of the cell. The nucleus (Fig. 76) has a definite membrane, a nucleolus, and a chromatic network.[1] Its division is mitotic.

Reproduction of cryptomonads is by longitudinal division and usually takes place while the cells are actively motile. Cell division is preceded by a division of the nucleus and a bipartition of gullet and vacuole.[2]

The two immobile genera have been placed in separate orders.[3] One of them has solitary angular cells surrounded by a thin firm wall:[4] the other[5] has ovoid cells united in amorphous palmelloid colonies containing an indefinite number of cells (Fig. 77*A*). Reproduction of both genera is by a formation of cryptomonad-like zoospores (Fig. 77*B*).

CLASS 2. DESMOKONTAE

The Desmokontae differ from other Pyrrophyta in that the wall of a cell is vertically divided into two halves (valves) that are without sub-

[1] Bělař, 1916, Reichardt, 1927; Ulehla, 1911. [2] Reichardt, 1927; Ulehla, 1911.
[3] Pascher, 1931. [4] Pascher, 1914. [5] Reinsch, 1911.

division into definitely arranged plates. Motile cells have two apically inserted flattened flagella that differ from each other in type of movement.

There are about six genera and 30 species; all rare organisms and most of them marine.

The dinophysoid dinoflagellates have been included[1] among the Desmokontae because their walls are vertically divided into two valves. However, recent studies[2] on valve structure among the dinophysids have shown that there is a series of definitely arranged plates, just as in "armored" dinoflagellates.

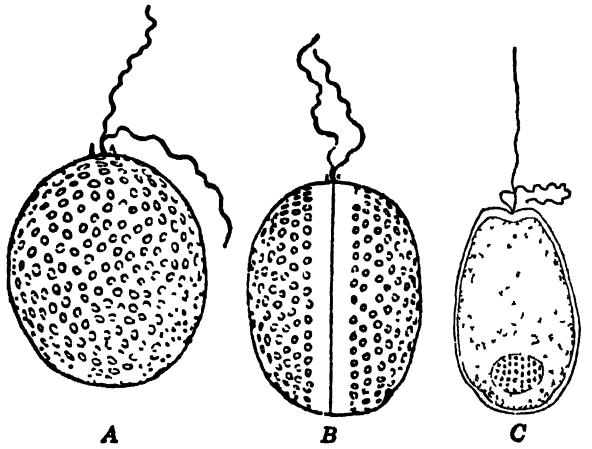


FIG. 78.—*Exuviaella marina* Cienk. *A-B*, surface views from front and side; *C*, optical section. (*A–B, from Schutt*, 1896; *C, after Klebs*, 1884) (*A B*, × 600, *C*, × 300.)

Some of the Desmokontae are naked and biflagellate, others are motile and have a wall. One genus is immobile and has a wall. Each of the three foregoing types has been made an order.[3]

Exuviaella, with about 10 species, is a marine flagellate with more or less compressed ellipsoidal cells (Fig. 78). Its protoplast is surrounded by a cellulose wall consisting of two longitudinally apposed valves.[4] Each valve has many small pores that are irregularly distributed over the entire surface except the marginal region apposed to the other valve. *Exuviaella* is biflagellate with the two flagella protruding through a common pore encircled by a ring of small teeth. One of the flagella projects vertically outward from the pore, and its lashing propels the cell through the water. The other flagellum stands at right angles to the propulsive flagellum (Fig. 78*C*). Its movement is undulatory and causes a rotation of the cell as it moves through the water.

[1] Fritsch, 1935; Pascher, 1927, 1931.
[2] Kofoid, 1926; Kofoid and Skogsberg, 1928; Tai and Skogsberg, 1932.
[3] Pascher, 1927, 1931. [4] Klebs, 1884, 1912; Schütt, 1890.

The protoplast contains two brownish laminate vertically elongate chromatophores, with or without pyrenoids. Reserve foods accumulate both in the chromatophores and in the cytoplasm. They include minute granules, probably of a starch-like nature, and small droplets of oil. There are two conspicuous vacuoles in the upper half of a protoplast, but they are not contractile. The single nucleus lies toward the posterior end of a cell.

Reproduction of *Exuviaella* is by longitudinal division. Each of the daughter cells receives one valve from the parent cell and secretes an entirely new one.

CLASS 3. DINOPHYCEAE

Cells of most Dinophyceae have a number of golden-brown to chocolate-brown discoid chromatophores that are with or without pyrenoids. Certain species lack chromatophores. The reserve foods are stored as starch or as oil. The cell wall, when present, contains cellulose, and in most motile genera (dinoflagellates) it consists of a definite number of articulated plates. Dinoflagellates and zoospores of immobile genera are encircled by a transverse groove (the *girdle*). The two flagella are inserted in or near the girdle; one of them encircles the cell transversely, the other extends vertically backward.

Reproduction of motile genera is usually by vegetative division, either while a cell is in motion or after it has come to rest. Motile genera may also produce aplanospores (cysts), and one of them is known to reproduce sexually. Reproduction of immobile genera may be by means of zoospores or aplanospores.

There are about 120 genera and 960 species, almost all of which are marine plankton organisms. Ninety per cent of the genera are dinoflagellates; the remainder are unicellular, palmelloid, or filamentous algae.

The Cell Wall. A majority of the dinoflagellates and all of the immobile genera have a definite wall. Walls of most species give a definite cellulose reaction, but there are certain species that do not seem to have cellulose in their walls.[1] The cell wall may consist of a single layer; or it may be differentiated into two layers, the outer of cellulose, the inner of unknown chemical composition.[2] Dinoflagellates rarely have the wall surrounded by a sheath of pectic material, but immobile genera generally have a pectic sheath.

Immobile genera and a few of the dinoflagellates have homogeneous walls. Almost all of the dinoflagellates have a wall composed of interlocking plates. The number and arrangement of plates are characteristic

[1] Schilling, 1891. [2] Mangin, 1907, 1911

of particular genera and species and are important diagnostic characters. The plates are usually covered with minute spines or with a fine reticulum of small ridges. These are not arranged in a definite pattern, but are usually more numerous near the margin than at the center of a plate.[1] The lines of juncture between plates, the *sutures*, are sometimes inconspicuous, but usually they are strongly evident and with a longitudinal or a transverse striation. As seen in cross section the abutting margins of plates may overlap each other, or they may be slightly infolded along the line of mutual contact.[2]

Structure of the Protoplast. Chromatophores of Dinophyceae are quite variable in color and in shape. A majority of species have rod-shaped, discoid, or irregularly band-shaped chromatophores at the periphery of the protoplast. Some species have a single stellate axial chromatophore with numerous radiating processes.[3] Many species have pyrenoids that may lie within the chromatophores or external to them.[4] Pyrenoids of Dinophyceae are similar to those of Chlorophyceae in that they have an encircling sheath of starch plates. The yellow-brown coloration of chromatophores has been ascribed[5] to the joint presence of a water-soluble brownish-red *phycopyrrin* and an alcohol-soluble reddish *peridinin*. According to another investigation[6] of the pigments, there is no phycopyrrin. The question of whether Dinophyceae have special pigments is in the same unsettled state as that of special pigments in Chrysophyceae, Bacillariophyceae, and Phaeophyceae. Some Dinophyceae also have a blue pigment, possibly similar in nature to the phycocyanin of Myxophyceae. This may be present in sufficient quantity to give the chromatophores a distinctly blue-green color.

Cells of Dinophyceae store their photosynthetic reserves as starch or as oils. As a general rule,[7] the chief food reserve of fresh-water species is starch and that of marine species is an oil. In some cases starch formation is associated with pyrenoids; in other cases there are no pyrenoids, and starch is deposited either in chromatophores or in the cytoplasm. "Unarmored" and "armored" dinoflagellates with chromatophores may also ingest solid foods, and this holozoic method of nutrition may be fully as important as the holophytic. Nutrition of species without chromatophores is holozoic or saprophytic. Algae and protozoa are among the most easily recognized of the ingested foods, and in some cases[8] the ingested organism may be about half the size of the dinoflagellate. The method by which armored dinoflagellates ingest food is not fully known, but it probably takes place by means of pseudopodia extruded from the girdle region.[9]

C

[1] Kofoid, 1909. [2] Werner, 1910. [3] Geitler, 1926. [4] Conrad, 1926.
[5] Schütt, 1890. [6] Kylin, 1927. [7] Killian, 1924; Klebs, 1912.
[8] Hofeneder, 1930; Woloszyńska, 1917. [9] Hofeneder, 1930.

Protoplasts of dinoflagellates usually contain two *pulsules*, but sometimes there are more or less evanescent accessory pulsules.[1] Pulsules bear a superficial resemblance to contractile vacuoles, but they have a distinct membrane and are noncontractile. A pulsule consists of a sac-like vacuole that is connected with the exterior of the cell by a slender canal opening into a flagellar pore of the cell wall. Pulsules are concerned with the intake of fluids and not, as might be supposed, with the discharge of liquids.[2]

All dinoflagellates and presumably all cells of immobile genera are uninucleate. The nucleus is surrounded by a distinct membrane and contains a conspicuous nucleolus. Early karyological studies describe[3] a reticulate arrangement of the chromatic material, but more recent investigations show[4] that the resting nucleus has moniliform chromatic

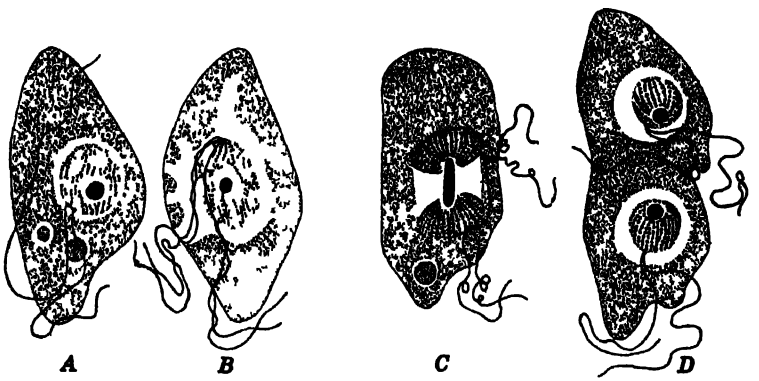


FIG. 79 —Cell division of *Oxyrrhis marina* Duj. (*After Hall*, 1925*A*) (× 1,170.)

threads with a parallel or spiral arrangement (Fig. 79). This arrangement persists even when the cells enter upon a resting aplanosporic condition. Nuclear division is mitotic and with or without a persistence of the nuclear membrane.

Many dinoflagellates and zoospores of most immobile genera have an eyespot. This is usually of simple structure, but in certain genera[1] there is a definite *ocellus* composed of two parts; a refractive hyaline lens and a surrounding pigment mass.

All motile cells are biflagellate and with laterally inserted flagella. One flagellum is thread-like and extends vertically backward from the point of insertion. It waves in a broad arc or with an active vibration of the distal end. The other flagellum is usually, if not always, ribbon-like[1] and lies in the girdle encircling the cell. It moves in a spiral or an

[1] Kofoid and Swezy, 1921. [2] Kofoid, 1909.
[3] Borgert, 1910; Jollos, 1910; Lauterborn, 1895.
[4] Entz, 1921; Hall, 1925; 1925*A*; Kofoid and Swezy, 1921.

undulatory manner. Two genera have been shown[1] to have a blepharoplast-rhizoplast-centriole type of neuromotor apparatus. The centriole is extranuclear and connected with two diverging rhizoplasts, each terminating in a blepharoplast. Nuclear and cell divisions are preceded by a bipartition of the neuromotor apparatus (Fig. 79). The centriole divides into two daughter centrioles that move to opposite poles of the nucleus. The two rhizoplasts, still attached to blepharoplasts and flagella, are distributed one to each daughter centriole. Shortly after their separation each of the daughter centrioles develops a second rhizoplast and blepharoplast.

Classification. Most systematic discussions of the Dinophyceae have been concerned with the dinoflagellates alone.[2] Such systems are inadequate because they do not take into consideration the immobile algal types derived from the dinoflagellates. There is a general agreement that the naked (unarmored) dinoflagellates are the most primitive of all Dinophyceae. It is also generally agreed that at least two series of armored dinoflagellates have been evolved from them. The immobile Dinophyceae also seem to have been evolved directly from the naked dinoflagellates. Their evolution from a motile unicellular ancestor is similar to that among Chlorophyceae, Xanthophyceae, and Chrysophyceae, and it has been proposed[3] that immobile Dinophyceae be divided into orders analogous to those in the three classes just mentioned. According to the foregoing bases, the motile genera fall into three orders and the immobile genera into four.

ORDER 1. GYMNODINIALES

The Gymnodiniales include all of the dinoflagellates with naked protoplasts or protoplasts with a homogeneous envelope that is not divided into plates. Vegetative cells are always motile and with two characteristic dinophycean flagella.

There are some 35 genera and 330 species, almost all of which are marine. Most of the marine species are free-swimming plankton organisms, but there are also a number of parasitic genera[4] that are either ecto- or endoparasites of various marine animals.

Free-swimming Gymnodiniales are usually solitary, but there is one genus where two, four, or eight cells are superimposed in permanent colonies.[5] Cells of Gymnodiniales are circular, oval, or subrhomboidal in front view, and circular to narrowly ellipsoidal in vertical view. Most species are naked, with the surface of the cytoplasm smooth or longitudinally

[1] Hall, 1925, 1925*A*.

[2] Kofoid and Swezy, 1921; Lindemann, 1928; Schütt, 1896; West, 1916.

[3] Pascher, 1927, 1931. [4] Chatton, 1920. [5] Kofoid and Swezy, 1921.

striated. A few fresh-water species have been described[1] as having a delicate wall composed of a large and indefinite number of small hexagonal platelets. All species have a transverse furrow (girdle), that is, a descending left-wound spiral, with the ends more or less widely separated from each other. The separated ends of a girdle are connected to each other by a vertical furrow (*sulcus*) that may project beyond the upper or lower ends of a girdle (Fig. 80). The flagella are inserted in the sulcus. The transverse flagellum is always inserted at the level of the upper end of the girdle; the longitudinal flagellum is variable in insertion, although usually below the level of the lower end of the girdle.

Most species have numerous discoid or bacilliform chromatophores but several species lack them.[2] The chromatophores are usually a golden brown, but they may be green, blue-green, or blue. Coloration of Gymnodiniales is not due entirely to chromatophores since the cytoplasm may also be tinged with colors covering nearly the whole range of the spectrum.

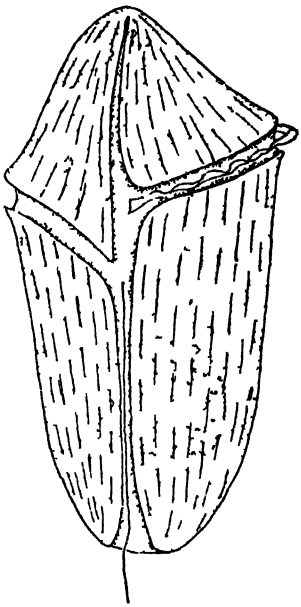


Fig. 80.—*Gymnodinium abbreviatum* Kofoid and Swezy (*After Kofoid and Swezy* 1921) (× 825)

Reproduction is usually by cell division and may take place while the cells are motile or immobile. The plane of division is generally vertical, but it may be transverse. Gymnodiniales may also form "resting cysts" that are comparable to the aplanospores of Chlorophyceae. The cysts are globose and surrounded by a definite wall. The entire protoplast of a cell generally develops into a single cyst, although it may divide to form two cysts.[3] The protoplast of a germinating cyst may develop into a single zoospore, or it may divide to form two or more zoospores. These may be liberated immediately or retained for some time within the gelatinized wall.

ORDER 2. PERIDINIALES

The Peridiniales include the dinoflagellates with a wall composed of a definite number of plates arranged in a specific manner, and in which the entire wall is never vertically separated into two halves or valves.

There are about 60 genera and 475 species, almost all of which are marine plankton organisms.

[1] Woloszyńska, 1917. [2] Kofoid and Swezy, 1921. [3] Klebs, 1912.

The transverse girdle divides the wall into two parts, *epitheca* and *hypotheca*, each with the plates in transverse bands or series.[1] Plates (Fig. 81) in the uppermost series of an epitheca are called *apical plates*,

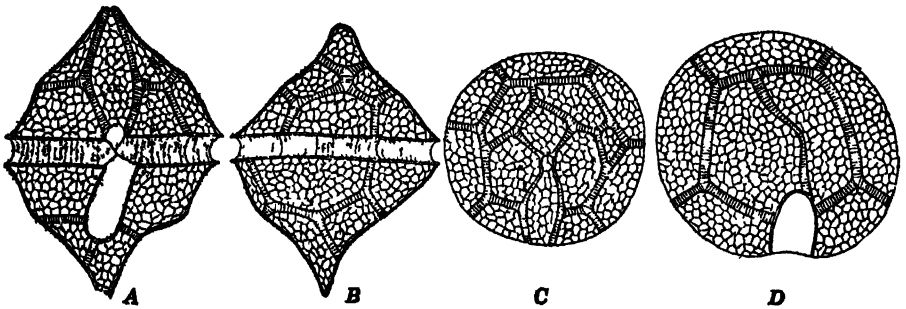


FIG 81.—*Peridinium wisconsinense* Eddy. (× 650.)

and those in the series adjoining the girdle are *precingular plates*. Some genera have an incomplete band of *anterior intercalary plates* between the apical and precingular series. In the hypotheca there is a series of

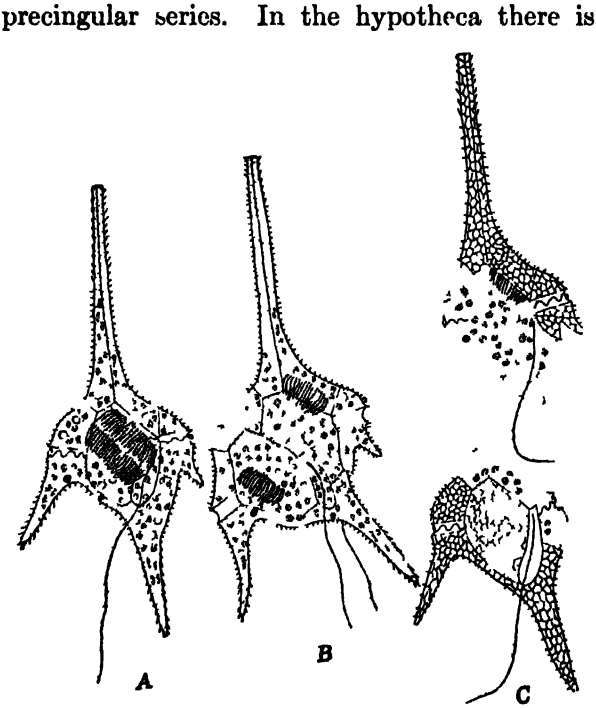


FIG. 82.—Cell division of *Ceratium hirundinella* (O F.M.) Schrank, showing the method of distribution of plates to daughter cells. (*After Lauterborn*, 1895.)

postcingular plates next to the girdle and one or two *antapical plates* below them. Occasionally there is a single *posterior intercalary plate* between the

[1] Kofoid, 1907, 1909.

two series. Many genera have a thin membranaceous *ventral plate* intercalated in the girdle region and extending through or into the pre- and postcingular series. The so-called ventral plate is really a series of small plates. The girdle is also made up of a series of curved plates.

Each of the two flagella emerges through a small pore in the region of the ventral plate. One is band-like and lies within the groove of the girdle; the other is thread-like, is straight, and extends toward the posterior end of a cell.

The protoplasts are uninucleate and almost always have many golden-brown chromatophores.

Reproduction of Peridiniales is usually by division into two daughter cells. This may take place either while the cells are actively motile

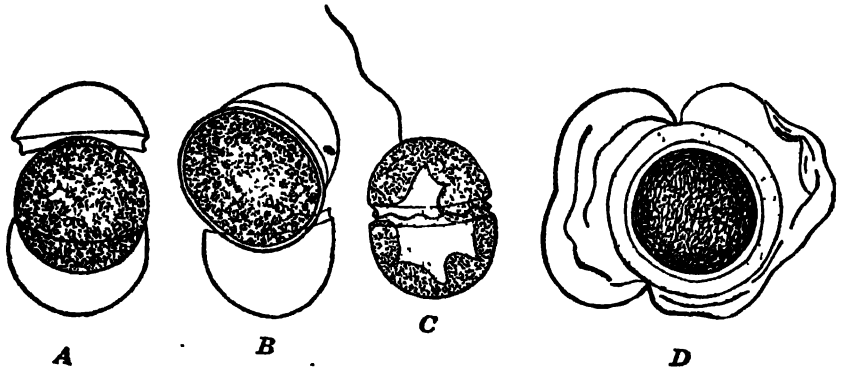


FIG. 83.—*A-C*, cysts and zoospore of *Glenodinium uliginosum* Schilling; *D*, cyst of *Hemidinium nasutum* Stein. (*A-C*, *from G. S. West*, 1909), *D*, *from Woloszynska*, 1925.)

or after they have come to rest. The plane of division is always more or less oblique, and each daughter cell may receive a portion of the parent-cell wall (Fig. 82), or the daughter protoplasts may escape from the old wall and develop entirely new walls. In the former case the parent-cell wall breaks in a specific manner and in such a fashion as to distribute certain epi- and hypothecal plates to each daughter cell. Peridiniales may also produce aplanospores ("resting cysts," Fig. 83).

The older literature on the Peridiniales contains several meager accounts of sexual reproduction, all of which are now thought to be based upon a misinterpretation of cell division. The description of a true conjugation in one of the genera (*Ceratium*)[1] was not generally accepted when first published, but recent confirmatory evidence[2] seems to show that this dinoflagellate does reproduce sexually. This takes place by two cells becoming apposed to each other, establishing a conjugation tube, and forming a zygote midway between the two old cell walls.

[1] Zederbauer, 1904. [2] Hall, 1925.

ORDER 3. DINOPHYSIDALES

The Dinophysidales are dinoflagellates with a wall composed of a definite number of plates arranged in a specific manner and with a wall that is vertically differentiated into two apposed halves (valves).

There are about 10 genera and 150 species, all marine and almost all of them plankton organisms.

The Dinophysidales have been referred[1] to the Desmokontae because the wall was thought to consist of two valves without a differentiation into plates. Both valves of a wall are now known[2] to consist of a specific number of plates arranged in a definite manner.

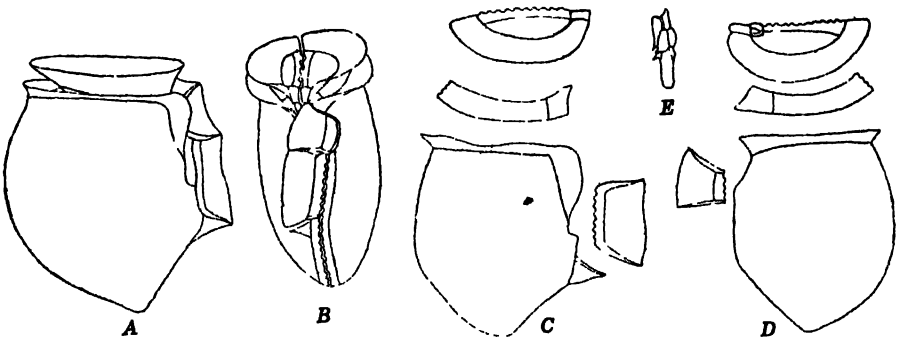


FIG. 84.—*Dinophysis acuta* Ehr. *A*, side view; *B*, ventral view; *C*, disarticulated plates of left-hand valve; *D*, disarticulated plates of right-hand valve; *E*, sulcal plates. (*Based upon Tai and Skogsberg*, 1934.)

Dinophysidales resemble Peridiniales in that a transverse girdle divides the wall into epi- and hypotheca but differ from them in that the epithecal portion is small and the hypothecal is very large. Dinophysidales also differ from Peridiniales in that there is regularly a development of conspicuous transverse wings by margins of epi- and hypotheca abutting on the girdle (Fig. 84). There may also be a conspicuous development of wings on the vertical zigzag saggital line (*suture*) where the two valves are apposed to each other. The wings have been considered[3] upturned margins of plates. Wings along the suture may be restricted to the ventral face of a cell (that bearing the flagella), or they may be upon both dorsal and ventral faces.

The wall always consists of 17 plates.[3] The epitheca is composed of five plates; a small symmetrical pair, a large symmetrical pair, and a single small asymmetrical *pore plate*. The girdle consists of two symmetrical pairs; one large, the other small. The hypotheca consists of eight plates; two symmetrical pairs, one very large and the other small,

[1] Fritsch, 1935; Pascher, 1931.

[2] Kofoid, 1926; Kofoid and Skogsberg, 1928; Tai and Skogsberg, 1934.

[3] Tai and Skogsberg, 1934.

and an asymmetrical group of four small platelets that lie in the longitudinal furrow (*sulcus*).

The arrangement of the flagella and the structure of the protoplast is as in the Peridiniales.

Reproduction is by longitudinal division. Each daughter protoplast receives one of the valves of the parent-cell wall and forms an entirely new half wall.

ORDER 4 RHIZODINIALES

The Rhizodiniales are Dinophyceae in which the vegetative cells are naked and amoeboid. The single known representative, *Dinamoebidium varians* Pascher,[1] is marine.

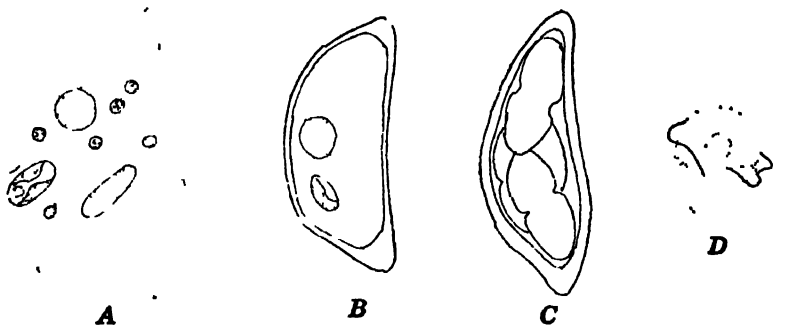


FIG. 85.—*Dinamoebidium varians* Pascher. *A*, amoeboid stage. *B*, resting cyst. *C*, germinating cyst. *D*, zoospores from a germinating cyst. (*After Pascher*, 1915.)

Dinamoebidium (Fig. 85) is an organism in which vegetative cells are permanently amoeboid, not temporarily so, as in certain Peridiniales. The protoplasts are without chromatophores but have a conspicuous nucleus. Amoeboid movement of cells is vigorous and due to a sending forth of plump pseudopodia somewhat shorter than those of *Amoeba proteus*. The nutrition of *Dinamoebidium* is holozoic, and its cells frequently contain unicellular algae and protozoa (Fig. 85*A*).

Vegetative division of the amoeboid stage has never been observed,[1] but a formation of temporary cysts takes place quite frequently. An amoeboid protoplast becomes spindle-shaped and secretes a gelatinous wall with a thickened cap at either pole (Fig. 85*B*). The encysted protoplast soon divides transversely, and each of the daughter protoplasts redivide once or twice. Cessation of division is followed by a metamorphosis of each daughter protoplast into a naked *Gymnodinium*-like zoospore with a single transverse flagellum (Fig. 85*C–D*). The zoospores are liberated by a softening of one pole of the enclosing cyst wall. Their shape changes continually as they swim about through the water.

[1] Pascher, 1916.

Swarming rarely lasts for more than 15 minutes; then the zoospores retract their flagella and become amoeboid.

ORDER 5. DINOCAPSALES

The Dinocapsales are palmelloid Dinophyceae with a temporary motile gymnodinoid stage. The order corresponds to the Tetrasporales of Chlorophyceae, Heterocapsales of Xanthophyceae, and Chrysocapsales of Chrysophyceae.[1]

The single member of the order, *Gloedinium montanum* Klebs, is fresh-water and found in peaty marshes. Its cells are large, subspherical, and are united in packet-like colonies by a common, concentrically stratified envelope (Fig. 86). The cells are uninucleate and contain many small brownish chromatophores that are sometimes radially arranged.[2] The protoplasts contain considerable starch, varying amounts of a colorless oily substance, and large droplets of an orange-red oil.

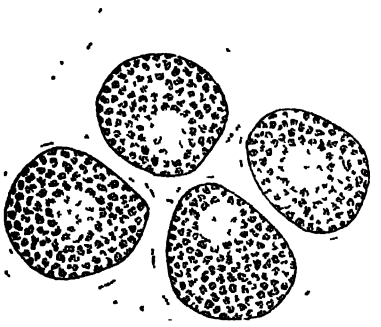


FIG. 86.—*Gloedinium montanum* Klebs (*After Klebs*, 1912) (× 510)

A cell divides vegetatively into two daughter cells that are retained within the enlarged envelope of the parent cell. This envelope usually persists until one or both of the two cells have divided. However, the colonies rarely develop beyond the four- or eight-celled stage because of gelatinization and degeneration of envelopes derived from the penultimate or antepenultimate cell generations.

In addition to multiplication by cell division there may be a reproduction by means of naked gymnodinoid zoospores.[3]

ORDER 6. DINOTRICHALES

The Dinotrichales are Dinophyceae in which the cells are immobile, more or less cylindrical, and joined end to end in branching filaments.

There are two genera, each with a single species.[1]

Filaments of one genus (*Dinothrix*, Fig. 87*A*) are the same diameter throughout; those of the other genus (*Dinoclonium*, Fig. 87*B*) are gradually attenuated toward the branch apices. Cell walls of Dinotrichales are stratified and contain cellulose. The protoplasts contain many small discoform chromatophores with a typical dinophycean color. Food reserves are stored either as starch or as oil.

[1] Pascher, 1927. [2] Killian, 1924; Klebs, 1912. [3] Killian, 1924.

Increase in length of a filament is due to transverse division of the cells. The two daughter protoplasts may at first have a gymnodinoid transverse furrow and an eyespot,[1] but these features disappear after each protoplast becomes invested with a wall layer of its own. Reproduction of Dinotrichales is due to a formation of *Gymnodinium*-like zoospores that are liberated through a pore in the lateral wall of a cell. The entire protoplast may develop into a single zoospore (Fig. 87*C*), or it

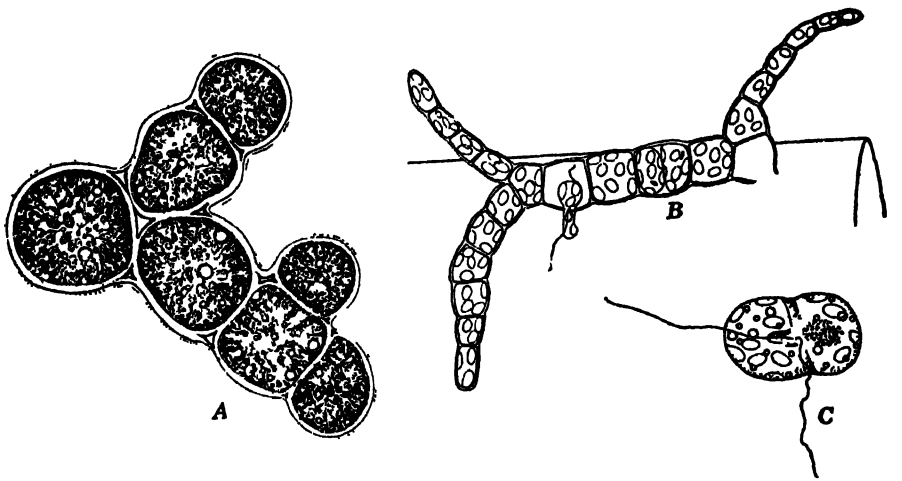


FIG 87.—Dinotrichales. *A*, filament of *Dinotrix paradoxa* Pascher. *B–C*, filament and zoospore of *Dinoclonium conradi* Pascher. (*From* Pascher, 1927.)

may divide to form two daughter protoplasts, each of which becomes a zoospore.

ORDER 7. DINOCOCCALES

The Dinococcales are unicellular immobile Dinophyceae in which there is no vegetative cell division and in which new cells are formed by a production of zoospores or aplanospores (autospores).

The order includes about 7 genera and 13 species, most of them freshwater.

The cells may be free-floating, or they may be sessile and attached to the substratum by a conspicuous gelatinous stipe.[2] Free-floating cells may be globose, lunate, or angular. Their protoplasts are uninucleate and with many discoform to rod-shaped golden-brown chromatophores (Fig. 88).

Reproduction is generally by a division of the protoplast into 2, 4, or 8 gymnodinoid zoospores. One species has been found[3] producing zooids of two different sizes, and there is a possibility that the smaller of the two

[1] Pascher, 1927. [2] Geitler, 1928; Klebs 1912; Pascher, 1927. [3] Pascher, 1928.

is gametic in nature. Zoospores (Fig. 88*B–C*) are usually liberated through a rent in the parent-cell wall They swarm for a comparatively short time, become immobile, assume the same shape as the vegetative cell, and secrete a homogeneous wall. Daughter protoplasts within a parent-cell wall may assume the shape characteristic of the species and secrete a wall before they are liberated from the old parent-cell wall.

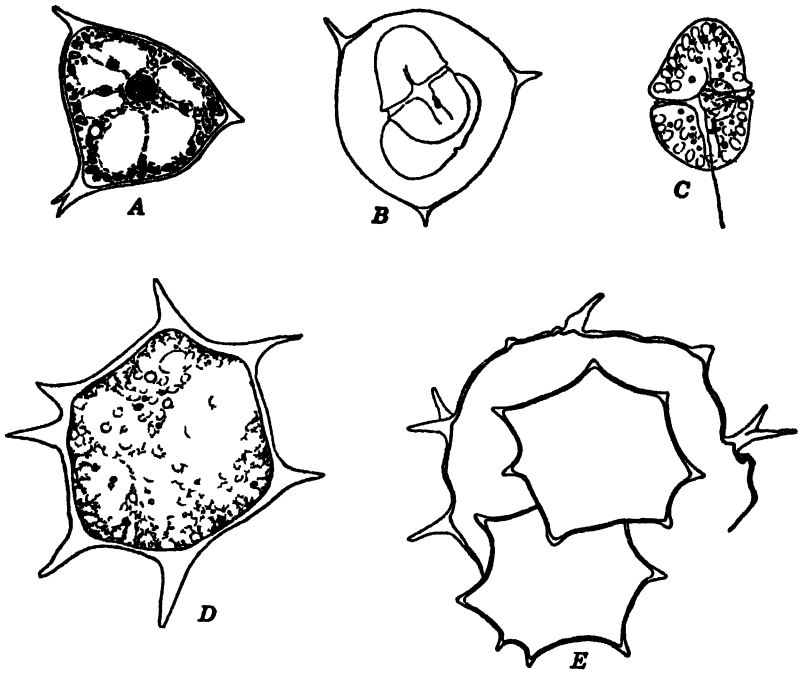


FIG 88.—Dinococcales. *A C Tetradinium minus* Pascher. *D E Dinastridium sexangulare* Pascher. (*From Pascher* 1927.)

Such aplanospores (Fig 88*E*) are comparable to the autospores formed by certain of the Chlorococcales

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CHAPTER V

CHRYSOPHYTA

The Chrysophyta have their pigments localized in definite chromatophores and have chromatophores in which there is a preponderance of yellowish or brownish carotinoid pigments. Food reserves accumulated include oils and leucosin (an insoluble carbohydrate of unknown composition). There is never a formation of starch. The cell wall is usually composed of two overlapping halves, and it is frequently impregnated with silica. The cells may be flagellated or nonflagellated, and solitary or united in colonies of definite form. Asexual reproduction may be by means of zoospores or aplanospores. Certain genera of each of the three classes are also known to have an endoplasmic production of a unique type of spore, the *statospore*. Sexual reproduction, when present, is isogamous and by a fusion of zoogametes or aplanogametes.

There are approximately 300 genera and 5,700 species. About three-fourths of the species are fresh-water.

Until recent years the Xanthophyceae (Heterokontae) were grouped with the Chlorophyceae; the Chrysophyceae were placed among the Flagellatae; and the Bacillariophyceae (diatoms) were placed in a series that was thought to be distantly related to the Phaeophyceae. The suggestion that Xanthophyceae, Chrysophyceae, and Bacillariophyceae are related to one another was first made by Pascher.[1] This was based upon similarities in pigmentation and food reserves, similarities in structure of cell walls, similarities in structure of motile stages, and the endoplasmic production of a distinctive type of spore. Data accumulated since then[2] have tended to show that these common features are widespread among the three. Phycologists are generally agreed that there is a relationship between Xanthophyceae and Chrysophyceae. They are less certain concerning the relationship of the Bacillariophyceae to them.

CLASS 1. XANTHOPHYCEAE

The Xanthophyceae (Heterokontae) have yellowish-green chromatophores in which carotinoids are present in greater amount than is chlorophyll. There is no formation of starch, and food reserves are stored as fats or as leucosin. The cell walls usually consist of two overlapping halves and rarely contain cellulose. The plant body may be unicellular or multicellular. Motile vegetative and reproductive cells are biflagellate,

[1] Pascher, 1914. [2] Pascher, 1921, 1924, 1937.

with two flagella of unequal length inserted at the anterior end. Asexual reproduction may be by means of zoospores or aplanospores. Several genera are also known to have an endoplasmic production of cysts (statospores). Sexual reproduction is of very rare occurrence and, when present, is isogamous and by a fusion of zoogametes.

There are about 60 genera and 150 species.

Distribution. A few genera are marine, the remainder are fresh-water. Fresh-water Xanthophyceae are usually aquatics but some of them are aerial. Certain aerial species grow on tree trunks, on damp walls, or intermingled with mosses and liverworts; other aerial species are terrestrial and grow intermingled with other algae of the soil or in dense stands on drying mud. Aquatic fresh-water species usually grow sparingly intermingled with other algae. Most of them grow in soft waters only.

Cell Structure. Cell walls of Xanthophyceae are composed chiefly of pectic compounds, either pectose or pectic acid. They may be somewhat impregnated with silica. Slight traces of cellulose have been found in walls of *Tribonema*,[1] and it has been held that the wall of *Botrydium*[2] consists almost wholly of cellulose Many genera have cells that are enclosed by walls with two overlapping halves that fit together as do the two halves of a bacteriologist's Petri dish. In unicellular genera the two parts may be of equal size or markedly unequal in length. The two-parted nature of a wall cannot usually be made out unless the cells have been treated with concentrated potassium hydroxide or with a strong (30 to 40 per cent) chromic acid solution. Detailed study[3] of the wall of one unicellular genus (*Ophiocytium*) has shown that the longer half consists of successive cup-shaped layers fitted one inside the other; the smaller half of the cell wall, the cover, is homogeneous in structure. In filamentous genera, as *Tribonema*, the wall of a filament is composed of a linear file of pieces that are H-shaped in optical section (Fig. 89). They alternately overlap one another so that each protoplast is enclosed by halves of two successive H-pieces. Each segment (H-piece) of a wall consists of two cup-shaped cylinders with a common base that constitutes a transverse wall of the filament. Each H-piece has a homogeneous H-shaped middle piece, the cross bar of the H constituting the median portion of the cell's cross wall, and the uprights of the H constituting the outermost layer of the lateral wall.[4] There are also additional layers of wall material lining the inner faces of the middle piece, and they lie so that each successively formed layer projects beyond the free margin of the previously formed one. The middle piece is the first-formed portion of a new wall segment, and the additional layers are successively deposited against it as a cell grows in length.

[1] Tiffany, 1924. [2] Miller, 1927; Pascher, 1937.
[3] Bohlin, 1897. [4] Bohlin, 1897; Tiffany, 1924.

Protoplasts of Xanthophyceae are generally uninucleate and with numerous discoid chromatophores. The only pigments within chromatophores are chlorophyll, which is present in small quantity, and carotinoids, which are present in abundance. The predominance of carotinoids over chlorophyll gives the chromatophore a characteristic yellow-green instead of a grass-green color Predominance of carotinoids is best demonstrated by the change to a blue-green color when the cells are heated in concentrated hydrochloric acid This color reaction affords one means of

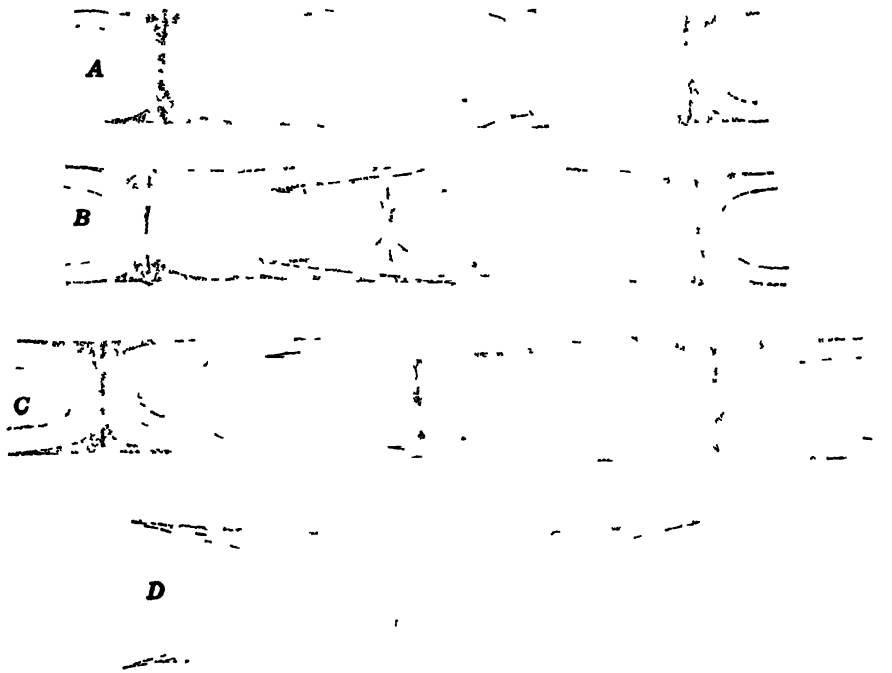


FIG 89.—Wall structure of *Tribonema bombycinum* (Ag.) Derbes and Sol. after treatment with potassium hydroxide. *A*, two *H*-pieces articulated to enclose a single protoplast. *B–C*, recently divided cells showing the intercalation of a new *H*-piece. *D*, *H*-piece (× 900)

differentiating between Xanthophyceae and Chlorophyceae since chloroplasts of the latter remain green or become yellowish green when treated in a similar fashion.[1] The amount of carotinoids in chromatophores is partially dependent upon external conditions, and in certain cases they do not develop in sufficient abundance to cause a typical color reaction when cells are treated with hydrochloric acid.[2] Chromatophores of most species are without pyrenoids, but those of certain species, as *Botrydium*, may have evident pyrenoids. Oil is the chief food reserve accumulated in protoplasts of Xanthophyceae, but leucosin, an insoluble white refrac-

[1] Bohlin, 1897; Poulton, 1925. [2] Geitler, 1930.

tive reserve of unknown chemical composition, is also a rather widely distributed food reserve.[1] In certain instances the formation of leucosin seems to be quite independent of photosynthesis and seems to be due to a saprophytic nutrition of the cell.[2] Not all white refractive granules within a protoplast are to be considered leucosin since some are probably excretory products.[3] This is especially true of old, slowly growing cells that contain numerous whitish granules. Little is known concerning the finer structure of the nucleus, but such nuclei as have been studied[4] possess a conspicuous nucleolus, a nuclear membrane, and considerable chromatic material.

Asexual Reproduction. Multiplication of tetrasporine and filamentous colonies may be purely vegetative and due to an accidental breaking

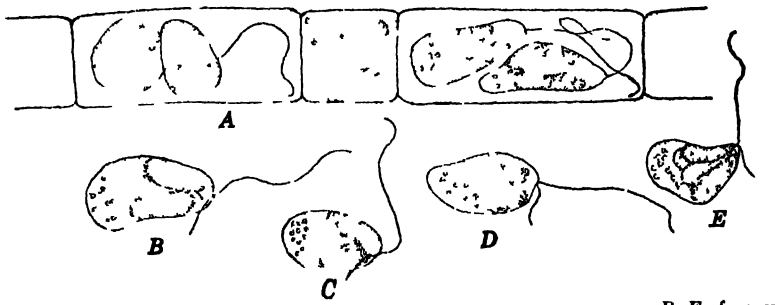


FIG. 90. *Bumilleria sicula* Borzi. *A*, filament containing zoospores. *B*–*E*, free-swimming zoospores. (× 900.)

of the colony into two parts; most of the genera that reproduce vegetatively and all genera without vegetative multiplication produce one or more types of spore.

Zoospores may be formed singly or in numbers within a cell. The zoospores are biflagellate, with the two flagella markedly different in length and inserted at the anterior end of the spore (Fig. 90). The longer flagellum, which is often four to six times longer than the shorter, extends straight ahead and is the propulsive organ of a zoospore. Staining by special methods shows that it is beset with a double row of delicate cilia. The shorter flagellum, sometimes called the "trailing flagellum," arises from the same point as the longer one and extends backward from the point of insertion. It is of the "whip" type and is without lateral cilia. Many of the descriptions of the xanthophycean zoospore as uniflagellate are due to a failure to observe the shorter flagellum, and one by one, genera which were thought to be uniflagellate have been shown to be biflagellate. Thus far, there has been no account of the method by which flagella are formed, and we cannot say whether or not their develop-

[1] Klebs, 1892; Molisch, 1923. [2] Lewis, 1913. [3] Pascher, 1925.
[4] Carter, 1919; Lewis, 1913. [5] Vlk, 1931.

ment is due to a neuromotor apparatus. Zoospores of Xanthophyceae are always naked, and they are usually pyriform. They generally contain one or more contractile vacuoles and more than one chromatophore. Eyespots are rarely present.

Instead of producing zoospores, the entire protoplast may develop into an aplanospore or divide into a number of parts, each of which becomes an aplanospore (Fig. 96*C–D*). In some cases, environmental conditions determine whether the alga shall reproduce by means of zoospores or by aplanospores. For example, *Botrydium* produces zoospores when it

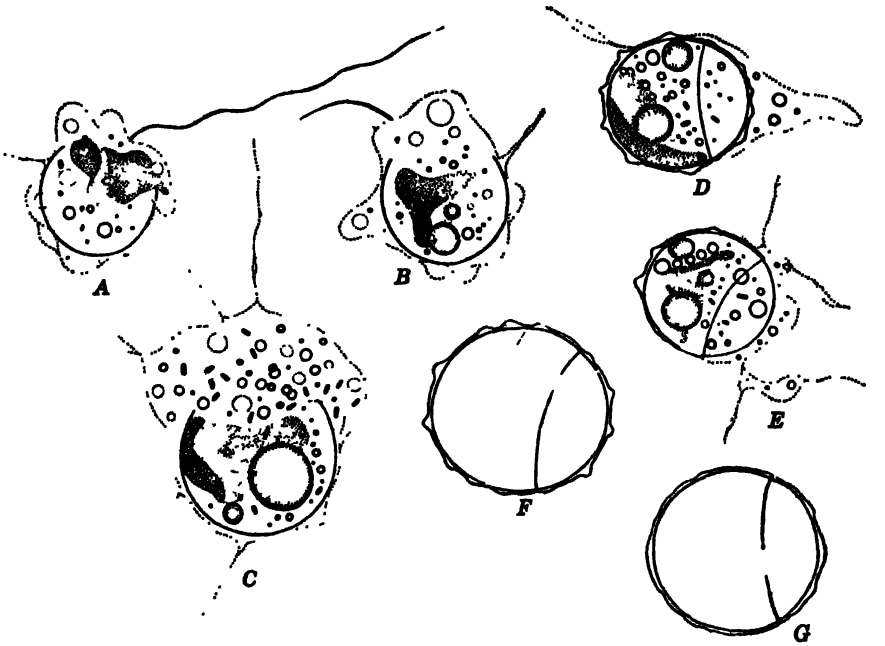


FIG. 91.—*Chloromeson agile* Pascher. *A–E*, stages in formation of statospores. *F–G*, walls of mature statospores. (*From Pascher*, 1932*A*.)

grows submerged and aplanospores when it grows on damp soil. Aplanospores may have walls that are homogeneous in structure or have walls composed of two overlapping halves. An aplanospore liberated from a parent-cell wall may grow directly into a new plant, or it may give rise to zoospores, which, in turn, grow into new plants.[1]

A few flagellated and rhizopodial Xanthophyceae are known[2] to form endoplasmic (endogenous) spores within their protoplasts. Such spores are usually called cysts, but they may also be called statospores because they seem to be homologous with statospores of diatoms. In the formation of a statospore there is an internal delimitation of a spherical proto-

[1] Borzi, 1895; Pascher, 1937. [2] Pascher, 1932*A*.

plast that is separated from the peripheral portion of the original protoplast by plasma membranes only (Fig. 91). The newly formed statospore then secretes a wall with two overlapping halves of equal or unequal size. Germinating statospores have their contents dividing to form two or four daughter protoplasts. The daughter protoplasts may be liberated as naked amoeboid bodies or as naked biflagellate zoospores.[1]

Sexual Reproduction. A union of motile gametes has been reported for a number of genera, but subsequent investigations have shown that many of these records are erroneous. Sexual reproduction by a fusion of isogamous zoogametes is definitely established for only two genera. In one of them (*Tribonema*)[2] one gamete in a uniting pair is immobile and the other motile; in the other genus (*Botrydium*)[3] both of a fusing pair

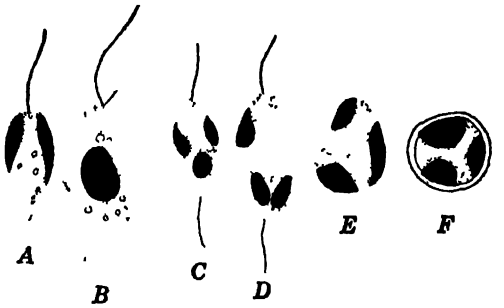


FIG. 92.--Sexual reproduction of *Botrydium granulatum* (L.) Grev. *A–B*, gametes. *C–D*, uniting gametes. *E F*, zygotes (*After Rosenberg*, 1930.)

are motile (Fig. 92). Nothing is known concerning the nuclear behavior after gametic union nor concerning zygote germination.

Evolution and Classification. Pascher was the first to point out[4] that the major evolutionary lines evident among the Chlorophyceae (page 25) are also evident among the Xanthophyceae. Beginning with a primitive motile unicellular type, there was an evolution of a tetrasporine colonial type, and this in turn lead to a filamentous type of plant body. There was also an evolution along the chlorococcine line in which the cells did not divide vegetatively, and one of the present-day genera (*Botrydium*) has attained a truly siphonaceous type of organization. There are no known Xanthophyceae with a volvocaceous type of organization. On the other hand, the Xanthophyceae include forms which have evolved along the rhizopodial line and in which the plant body is of a naked plasmodial type.

The Xanthophyceae are segregated into orders on the same basis as the Chlorophyceae,[5] and most of the orders have their counterpart among the Chlorophyceae. The Heterochloridales are comparable to the

[1] Pascher, 1932*A*. [2] Scherffel, 1901. [3] Rosenberg, 1930.
[4] Pascher, 1913. [5] Pascher, 1913, 1925.

Volvocales, the Heterocapsales to the Tetrasporales, the Heterotrichales to the Ulotrichales, the Heterococcales to Chlorococcales, and the Heterosiphonales to Siphonales.

ORDER 1. HETEROCHLORIDALES

The Heterochloridales include all Xanthophyceae with flagellated vegetative cells. All genera are unicellular and without cell walls. The protoplasts contain two or more discoid or bacilliform chromatophores and one or more contractile vacuoles. Reproduction is by cell division. One genus is known to form statospores.

The order includes about eight genera, each with a single species. All but one of them are fresh-water, and all are very rare species.

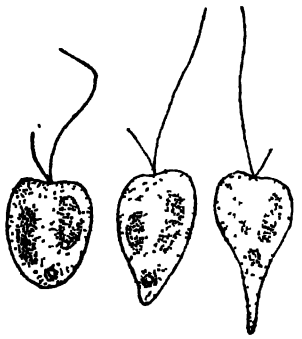


FIG. 93.—*Chlorochromonas minuta* Lewis. (× 2,000.)

Cells of all genera show a marked tendency to change from a flagellated to an amoeboid stage, and many of them, when in an amoeboid state, supplement their autotrophic nutrition by engulfing solid foods. Cell division may take place while the cells are actively motile or after they have passed into temporary palmelloid or amoeboid stages.

Chlorochromonas, with the single species *C. minuta* Lewis (Fig. 93), is a fresh-water flagellate. Its solitary cells are generally free-swimming; although sometimes either amoeboid or sessile, and attached to the substratum by a posterior pseudopodium-like process. Motile cells are pyriform to subovoid and have two flagella of unequal length inserted in an oblique depression at the anterior end.[1] The longer flagellum is about twice as long as the cell; the other about half the length of a cell. The naked protoplast contains two yellowish-green curved chromatophores (with their concave faces apposed), a single contractile vacuole laterally located near the anterior end, and a single centrally located nucleus. The major portion of the food reserves are accumulated in a single large leucosin granule in the posterior end of a cell, but there may be, in addition, minute droplets of oil in the cytoplasm.

Reproduction is by longitudinal division and takes place while the cells are in a motile state.

ORDER 2. RHIZOCHLORIDALES

The Rhizochloridales have amoeboid protoplasts with pseudopodia. The protoplasts may be solitary or joined to one another by cytoplasmic bridges. Solitary protoplasts may be naked or partially surrounded by

[1] Lewis, 1913; Smith, G. M., 1933.

an envelope (*lorica*) that may be sessile and attached to the substratum by a stipe. The protoplasts are uninucleate or multinucleate and have one to several chromatophores

Reproduction is by vegetative division or by a division of the protoplast into zoospores The entire protoplast may round up, secrete a wall, and become aplanospore-like; or it may have an endoplasmic formation of statospores

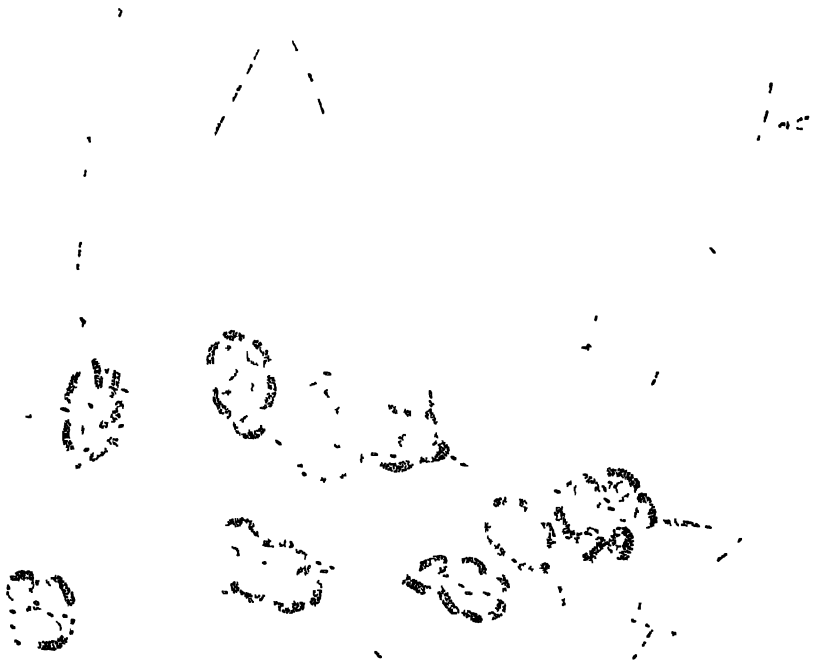


FIG. 94 *Chlorarachnion reptans* Geitler (*After Geitler*, 1930*A*)

The order contains about 7 genera and 10 species, most of which are fresh-water

The Rhizochloridales are Xanthophyceae in which the vegetative cells are permanently amoeboid instead of temporarily so as in the Heterochloridales The amoeboid protoplasts may separate from one another immediately after division, or they may remain united by cytoplasmic strands until they have become plasmodial masses with as many as 150 cells.[1] Protoplasts of most Rhizochloridales are uninucleate, but those of at least one genus[2] are multinucleate In some genera the only known method of reproduction is a vegetative division into two daughter proto-

[1] Geitler, 1930*A*. [2] Pascher, 1930*A*

plasts.[1] In the only known multinucleate genus the protoplast may divide to form several zoospores.[1] This may take place while the protoplast is in a vegetative condition or after it has rounded up and secreted a wall. Endoplasmic statospores are also known for this genus, and they have been shown[2] to form zoospores when they germinate.

Chlorarachnion, a marine genus with the single species *C. reptans* Geitler (Fig. 94), is the largest of all Rhizochloridales. It is a naked plasmodium one cell in thickness, with as many as 150 cells joined to one another by long cytoplasmic bridges.[3] The multicellular body may creep slowly in a plasmodial fashion across the bottom of a culture dish, or it may be free-floating. The individual cells have a single centrally located nucleus and a half-dozen or more disk-shaped chromatophores. Most of the chromatophores in a cell contain a conspicuous pyrenoid. Chromatophores are never present in the cytoplasmic strands connecting cells one to another. The protoplast also contains minute granules, presumably particles of reserve food. Nutrition of a plasmodium is partly autotrophic and partly holozoic by a mass ingestion of diatoms or other unicellular algae.

Multiplication is exclusively by cell division, and division may take place in either peripheral or interior cells of a plasmodium.

ORDER 3. HETEROCAPSALES

The Heterocapsales include those palmelloid Xanthophyceae whose immobile vegetative cells have the ability to return directly to a motile condition, or whose zoospores have the ability to divide directly into new zoospores. Immobile vegetative cells are surrounded by a gelatinous envelope that unites them in amorphous or dendroid colonies containing an indefinite number of cells. Cells of Heterocapsales have characteristically yellowish-green chromatophores and, so far as known, only fats and leucosin as reserve foods.

Reproduction, aside from vegetative cell division, is by means of naked zoospores. Thick-walled akinetes may also be formed.

The order contains about eight genera and nine species, all fresh-water.

Chlorosaccus, with the single species *C. fluidus* Luther, has spherical to subspherical colonies that may be 20 mm. or more in diameter. The colonies are a very pale yellowish-green, and they may be free-floating or attached to submerged aquatics (Fig. 95*A*). The cells are ellipsoidal and lie irregularly distributed within the homogeneous gelatinous colonial matrix (Fig. 95*B*). Each cell contains two to six disk-shaped chromatophores, a single nucleus, and two to four leucosin granules.

Reproduction is by a direct metamorphosis of vegetative cells into elongate naked zoospores with two flagella of unequal length at the

[1] Geitler, 1930*A*; Pascher, 1932. [2] Pascher, 1932*A* [3] Geitler, 1930*A*.

anterior end.[1] The zoospores are generally liberated during the early morning hours. After swarming for a few hours, they come to rest, withdraw their flagella, and secrete a thin wall with a rather broad gelatinous envelope. The one-celled germling increases in size and then divides into four daughter cells, each with a somewhat indistinct gelatinous sheath. Cell division and redivision may continue indefinitely. Sometimes the cells develop into akinetes with thick walls, more numerous chromatophores, and an abundant content of reserve food.[2]

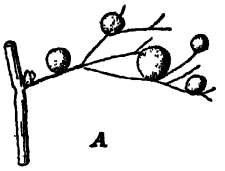




FIG. 95.—*Chlorosaccus fluidus* Luther. *A*, colonies epiphytic upon *Ranunculus aquatilis* L. *B*, portion of a thallus. (*A*, × ½; *B*, × 600.)

ORDER 4. HETEROTRICHALES

The Heterotrichales include all of the Xanthophyceae with the cells united end to end in simple or branching filaments. Asexual reproduction may be by means of zoospores, aplanospores, or akinetes. One genus is known to reproduce sexually by a union of zoogametes.

There are about 7 genera and 17 species, all fresh-water.

Tribonema, with some eight species, is a widely distributed fresh-water alga that frequently grows in abundance in temporary pools during the early spring. Its cells are cylindrical or barrel-shaped, two to five times longer than broad, and joined end to end in unbranched filaments of indefinite length (Fig. 96*A*). The manner in which the H-pieces of the wall are articulated, and their structure, have already been discussed (page 169). The protoplast of a cell is uninucleate and, according to the species, contains few or many discoid chromatophores. Pyrenoids are lacking and photosynthetic reserves are stored as oils or granules of leucosin, never as starch. Old protoplasts often have numerous small refractive granules within the cytoplasm; the majority of which are probably waste products.

Asexual reproduction may be purely vegetative and result from an accidental breaking of filaments or from a disarticulation of certain H-pieces at the time of spore liberation.

[1] Luther, 1899; Smith, G. M., 1933. [2] Luther, 1899.

Reproduction by means of aplanospores appears to be of much more frequent occurrence than reproduction by means of zoospores. Aplanospores[1] may be formed singly within a cell or more than one may be formed (Fig. 96*C–D*). The aplanospores are liberated by a pulling apart of H-pieces of the old parent-cell wall. Aplanospores generally have a wall consisting of two overlapping halves. Germination of an aplanospore is direct and begins with a separation of the two halves of the wall due to an elongation of the protoplast; then the elongating protoplast becomes cylindrical in shape and secretes a wall distinct from the old aplanospore wall.[2] *Tribonema* may also form akinetes. They are usually formed in several successive cells of a filament.

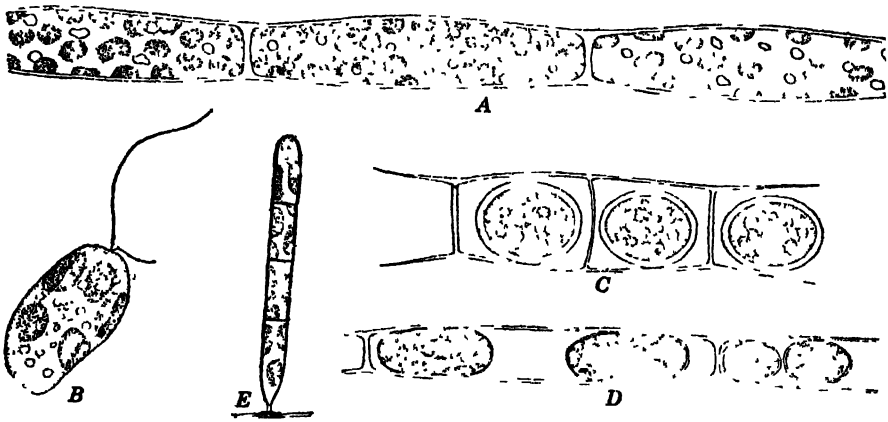


FIG. 96.—*Tribonema bombycinum* (Ag.) Derbes and Sol. *A*, portion of a vegetative filament. *B*, zoospore. *C D*, aplanospores. *E*, germling. (*A*, *D E*, × 600; *B*, × 975, *C*, × 650.)

Zoospores (Fig. 96*B*) are generally formed singly within a cell. They are naked, are pyriform, contain two to several chromatophores, and have two flagella of unequal length at the anterior end.[3] A zoospore swarms for a short time and then comes to rest (possibly with the flagellated end downward) and secretes a wall which is attached to the substratum by a brownish discoid holdfast. One-celled germlings look very much like certain sessile unicellular Heterococcales, but this resemblance ceases after they have divided transversely and begun to grow into filaments (Fig. 96*E*). Sooner or later a developing filament, or the distal portion of it, breaks away and continues growth as a free-floating alga.

Sexual reproduction is isogamous and by the fusion of zoogametes.[4] One of a pair of gametes comes to rest and withdraws its flagella just before the other swims up to and unites with it.

[1] Lagerheim, 1889; Poulton, 1925; Wille, 1881. [2] Lagerheim, 1889.
[3] Luther, 1899; Pascher, 1925; Poulton, 1925; West, 1904. [4] Scherffel, 1901.

ORDER 5. HETEROCOCCALES

The Heterococcales include the nonfilamentous Xanthophyceae in which the immobile vegetative cells are surrounded by a wall and are not capable of returning directly to a motile condition. Vegetative cells are uninucleate or multinucleate. They have typical chromatophores and food reserves, and many of them have walls with two overlapping halves. Some genera are unicellular; others are multicellular and have the cells embedded within a common gelatinous matrix.

Reproduction may be by means of zoospores or aplanospores (autospores).

There are about 35 genera and 85 species, almost all of which are found in fresh waters.

The Heterococcales correspond to the Chlorococcales of the Chlorophyceae, and several genera with a distinctive cell shape have their corresponding genera among the Chlorococcales. In fact, many of the species were assigned to various genera of Chlorococcales when first described. There are reasons for believing that, similar to Chlorococcales, cells of Heterococcales do not divide vegetatively. This is certainly true of unicellular genera. It is more difficult to demonstrate among colonial genera, because it is sometimes impossible to distinguish between a purely vegetative division and a division of the protoplast into two aplanospores or autospores.

Botrydiopsis, with about four species, is a widely distributed terrestrial alga, but one frequently overlooked because it rarely occurs in sufficient quantity to form a conspicuous coating on the soil. The cells are always solitary. They are usually spherical, but they may be asymmetrical or biscuit-shaped. The wall of a cell is relatively thin and composed of two overlapping halves[1] that are sometimes slightly silicified.[2] A very young cell contains one or two discoid chromatophores; as the cell grows in size the chromatophores increase in number, and an adult cell may contain more than a hundred of them (Fig. 97*A–E*). Pyrenoids have been observed in stained cells of one species.[3] The food reserves are stored as minute droplets of oil.[4]

Zoospore formation may take place at any stage in the growth of a cell. When produced by young cells, only four or eight zoospores are formed; when produced by adult cells, they are formed in large numbers. The zoospores are broadly ovoid to pyriform, naked, and with two flagella of unequal length at the anterior end.[5] They contain one or two chromatophores, and possibly have an eyespot (Fig. 97*F*).

[1] Pascher, 1915. [2] Pascher, 1925 [3] Korshikoff, 1930.
[4] Borzi, 1895; Pascher, 1937; Poulton, 1925.
[5] Chodat, 1913; Luther, 1899; Poulton, 1925; Smith, G. M., 1933; Vlk, 1931.

Frequently, and possibly because of environmental conditions, the cells form aplanospores instead of zoospores. The aplanospores, similar to zoospores, generally grow directly into vegetative cells. Sometimes, however, an aplanospore develops a very thick wall and has a greater content of food reserves than is ordinarily the case.[1] Such hypnospores

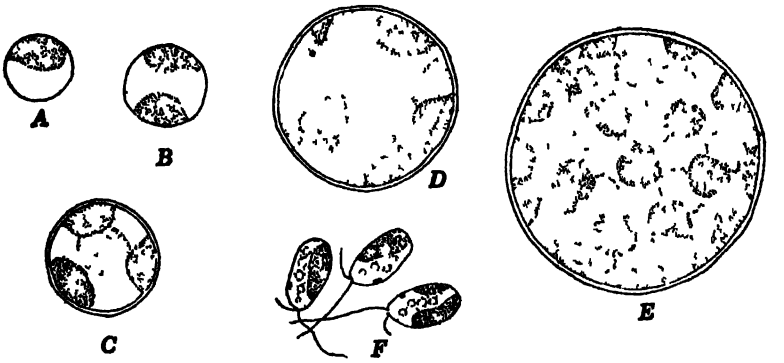


FIG. 97.—*Botrydiopsis arhiza* Borzi. *A–E*, vegetative cells. *F*, zoospores. (× 900)

appear to enter into a period of rest before their contents divide to form either zoospores or aplanospores.

ORDER 6. HETEROSIPHONALES

The Heterosiphonales include the multinucleate siphonaceous Xanthophyceae.

There is but one genus, *Botrydium*. It has four species, all of them terrestrial and growing either on drying muddy banks of streams and pools or on bare damp soil. If conditions are favorable, the alga may form an extensive green coating on the soil.

The unicellular multinucleate plant body consists of a vesicular aerial portion, which contains the chromatophores, and a colorless rhizoidal portion which penetrates the soil (Fig. 98*A–B*). The aerial portion may be 1 to 2 mm. in diameter. In three species it is more or less globose; in the fourth it is a forked cylinder. Species whose aerial portions are usually globose are considerably influenced by environmental conditions, and the aerial portion may be an elongated cylinder if the plant grows in shaded habitats.[2] The vesicular portion has a relatively tough wall and internal to this a thin layer of cytoplasm containing many nuclei and chromatophores. The chromatophores are discoid and often connected to one another by strands of denser cytoplasm. Pyrénoid-like bodies are often present in chromatophores of young plants, but there is never any starch in the protoplast and photosynthetic reserves accumulate as oils or as leucosin. The rhizoidal portion, which may be profusely or spar-

[1] Borzi, 1895; Poulton, 1925. [2] Kolkwitz, 1926.

ingly branched, is without chromatophores but contains many nuclei scattered through the vacuolate or nonvacuolate cytoplasm.

Cells of *Botrydium* do not divide vegetatively, and the only method by which new plants may be formed is through a production of zoospores, aplanospores, or zygotes. Zoospore formation usually takes place during rainy weather. The contents of the vesicular portion become divided into innumerable uninucleate protoplasts, each of which becomes metamorphosed into a pyriform zoospore with two flagella of unequal length

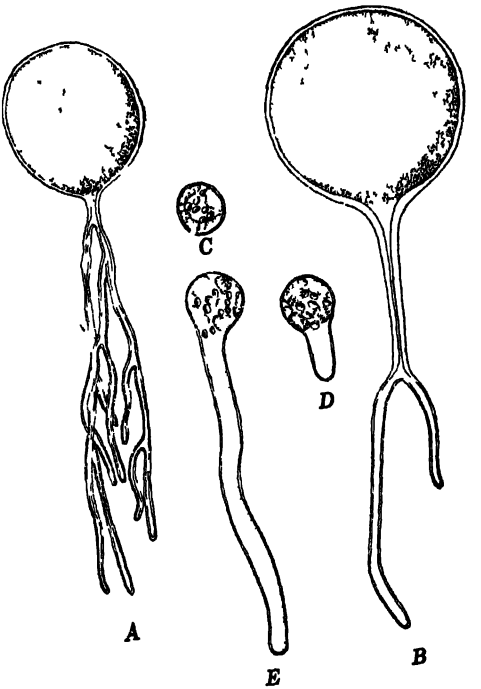


FIG. 98.—*A*, *Botrydium granulatum* (L.) Grev. aplanospores of *B granulatum* *B*, *B Wallrothii* Kutz *C–E*, germinating (*A–B*, × 25, *C–E*, × 310)

at the anterior end.[1] The method by which zoospores escape from the parent-cell wall is not definitely known, but it seems to be accomplished by a gelatinization of the apical portion of the wall.

When *Botrydium* is growing on rather dry soil, there is usually a formation of aplanospores instead of zoospores (Fig. 98*C*). In many cases the aplanospores are formed in the same fashion as are zoospores, and they represent zoospores that have formed a cell wall before leaving the old parent-cell wall. In other cases, as in *B. Wallrothii* Kutz., there is a cleavage of the cell contents into multinucleate protoplasts which become rounded and secrete a wall. These coenocytic aplanospores (coenocysts)

[1] Kolkwitz, 1926; Miller, 1927; Pascher, 1937· Poulton, 1930.

are not the morphological equivalent of zoospores. Both types of aplanospore develop directly into new plants (Fig. 98*D–E*).

Aplanospores may become thick-walled resting spores (hypnospores). In some cases the hypnospores are formed in the aerial portion of the cell and are either uninucleate or multinucleate. In other cases practically all of the protoplasm of the aerial portion migrates into the rhizoids and there becomes divided into a number of multinucleate, serially arranged portions, each of which becomes a hypnospore.[1] In one species a single hypnospore is formed at the end of each branch in the rhizoidal system.[2] Uninucleate hypnospores develop directly into new plants. Multinucleate ones have their protoplasts dividing to form a number of zoospores or aplanospores.[3]

The protoplast of the vesicular portion may also divide to form biflagellate zoogametes. *Botrydium* is homothallic and gametic union may take place before liberation from the parent-cell wall.[4] The gametes are pyriform to broadly ellipsoidal, and their posterior ends become apposed at the time they fuse in pairs. The zygote is spherical and has a fairly thick wall (Fig. 92). It germinates directly into a new plant.

CLASS 2. CHRYSOPHYCEAE

The Chrysophyceae have cells with a small number of yellowish- or golden-brown chromatophores that usually lack pyrenoids. Food reserves include both fats and leucosin, but there is never a storage of starch. The cells may be flagellated or immobile, and naked or surrounded by a wall. They may be solitary or united in colonies of definite form. Motile vegetative cells and zoospores have their flagella inserted at the anterior end. They may be uniflagellate or biflagellate; in the latter case the flagella may be of equal or unequal length. Many members of the class produce endoplasmic statosphores enclosed by a two-parted silicified wall with a terminal pore. Sexual reproduction is not definitely established for any member of the class.

There are some 65 genera and 210 species.

For a long time the only known members of the class were motile organisms whose relationships were thought to be more within the protozoa than with the algae. Within the past two decades, especially through the investigations of Pascher,[5] there has been a discovery of a considerable number of immobile coccoid and filamentous Chrysophyceae with a truly algal organization.

Distribution. A very large proportion of the species are fresh-water, and most of them are found only in soft waters and at seasons of the year when the water is cool. Many of the motile fresh-water species are found

[1] Miller, 1927; Rostafiński and Woronin, 1877. [2] Iyengar, 1925.
[3] Miller, 1927. [4] Rosenberg, 1930. [5] Pascher, 1925*A*, 1931*A*, 1931*B*, 1931*C*.

in the plankton of lakes, where they are often present in abundance. The coccoid and filamentous genera are found mostly in cold springs and brooks, especially in mountainous regions, where they occur as gelatinous or crustaceous growths on stones and woodwork. Many of the Chrysophyceae are very sensitive to changes in the environment and completely disintegrate within a few hours after they are brought into the laboratory.

Cell Structure. Most of the flagellated Chrysophyceae, the *chrysomonads*, have naked protoplasts. Others have their protoplasts completely surrounded by a sheath of pectic material that may contain siliceous scales. Still other chrysomonads have their protoplasts surrounded by an open rigid envelope (*lorica*) separated from the protoplast by an intervening space. Coccoid and filamentous Chrysophyceae have firm, closely fitting walls. Walls of vegetative cells rarely have an evident differentiation into two overlapping halves.

A majority of genera have protoplasts that contain but one or two golden-brown chromatophores. The golden-brown color has been ascribed to an accessory pigment (*chrysochrome*[1] or *phycochrysin*[2]) which overlies the chlorophyll and associated carotinoids The presence of a special pigment in Chrysophyceae, as in Bacillariophyceae, is somewhat questionable. Pyrenoid-like bodies are present in chromatophores of certain genera, but their function is not known. Nutrition of Chrysophyceae may be wholly autotrophic or, if the protoplasts are naked, partly autotrophic and partly heterotrophic. Food reserves may accumulate either as fats, leucosin, or volutin; but never as starch. Leucosin, whose chemical composition is unknown, is laid down in the form of white refractive granules which generally accumulate in the cytoplasm.[3] The volutin described as being present in Chrysophyceae.[4] may be identical with leucosin. Glycogen has been found[5] in the statospores (cysts) of one genus.

Many of the motile forms have contractile vacuoles at the base of the flagella, and these vacuoles persist even after the flagellated phase has passed over into a temporary amoeboid phase. Although the chrysomonads are the only members of the class whose cells have been studied cytologically, it is rather probable that all Chrysophyceae are uninucleate. In the genera investigated,[6] the nuclei have a distinct nucleolus and, as a rule, conspicuous chromatin granules. Nuclear division is mitotic and by means of a spindle that is intranuclear in origin. The nuclei are so small that the details cannot be made out with certainty, but there appears to be an equational halving of the chromosomes that lie on the equator of a spindle. Centrosomes have been observed in association with the spindles, but the relationships between centrosome and neuro-

[1] Klebs, 1892. [2] Gaidukov, 1900. [3] Klebs, 1892; Molisch, 1923.
[4] Doflein, 1923. [5] Conrad, 1927. [6] Conrad, 1927; Doflein, 1916, 1918.

motor apparatus are obscure. One genus has been shown[1] to have a complicated neuromotor apparatus with a rhizoplast connecting a large extranuclear granule with the flagellum. Flagella have been studied in detail only in genera with two flagella of unequal length. The longer of the two bears short, diagonally inserted cilia on all sides; the shorter is of the whip type.[2]

Asexual Reproduction. Cell division in unicellular flagellate genera is always longitudinal and into two daughter cells that immediately separate from each other. Multiplication of colonial motile genera may be by a colony fragmenting into two or more parts, or by a single cell breaking away from the colony and developing into a new colony. Coccoid and filamentous nonmotile colonies may reproduce by vegetative fragmentation.

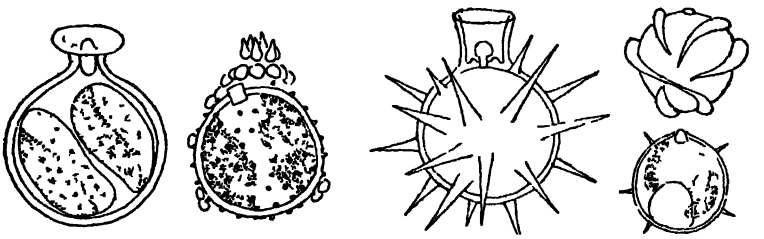


FIG. 99.—Statospores of Chrysophyceae. *A*, *Chromulina Pascheri* Hofeneder. *B*, *Mallomonas coronata* Bolochi. *C*, *Ochromonas stellaris* Dofl. *D*, *Cellonella palensis* Pascher (*A*, *after Conrad*, 1926, *B*, *after Conrad*, 1927, *C*, *after Doflein*, 1922, *D*, *after Pascher*, 1929)

All of the Chrysophyceae except the chrysomonads may produce zoospores. These are usually formed singly within a cell but in certain genera[3] the protoplast divides to form several zoospores. Zoospores of Chrysophyceae are naked and have one or two chromatophores. Some are uniflagellate;[4] others are biflagellate and have flagella of either equal[4] or unequal[5] length. None of the Chrysophyceae produces aplanospores.

The unique type of spore—the statospore or cyst—produced by Chrysophyta is known for many genera of Chrysophyceae. Statospores of Chrysophyceae are usually spherical, although sometimes ellipsoidal. The spore wall is silicified, composed of two overlapping halves, and has a small circular pore closed by a conspicuous plug that may or may not be silicified. Statospores of many species have a smooth wall and a simple plug[7] or have the margin of the pore elevated into a flange-like collar (Fig. 99). Those of other species have walls ornamented with punctae, spines, or flange-like plates. As is the case with zygotes of Desmidiaceae, no one type of sculpturing is characteristic for a particular genus, and

[1] Conrad, 1927. [2] Petersen, 1929. [3] Pascher, 1931*B*.
[4] Conrad, 1922; Pascher, 1925*A*, 1929, 1931*A*, 1931*B*. [5] Lagerheim, 1884.
[6] Pascher, 1925*A*. [7] Conrad, 1922, 1927; West, 1904.

there may be marked differences in ornamentation from species to species in a genus.

Most investigations of statospore formation have been upon chrysomonads,[1] but certain nonmotile genera are also known[2] to have an endoplasmic formation of them. A motile cell about to form a statospore comes to rest, retracts its flagella, and assumes a spherical shape. There is then an internal differentiation of a spherical protoplast that is separated only by plasma membranes from the peripheral portion of the original protoplast (Fig. 100*A–E*) Following this, there is a secretion

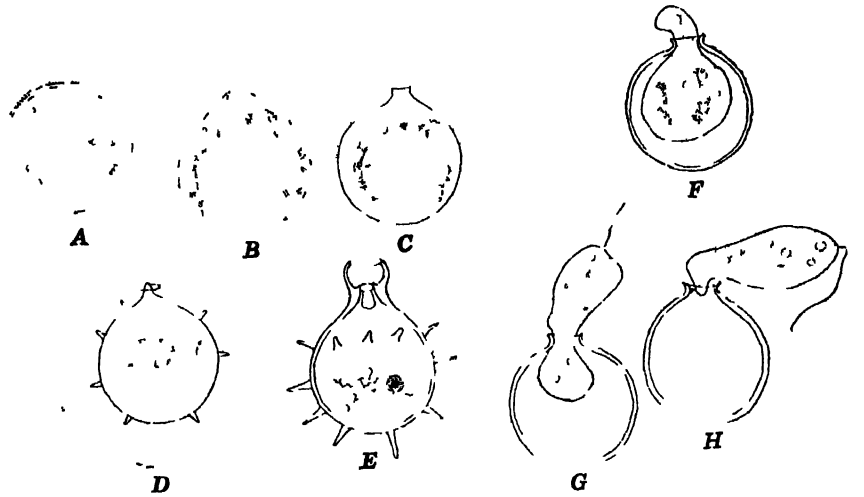


FIG. 100 —*A–E*, statospore formation in *Ochromonas crenata* Klebs *F–H*, germination of statospore of *Chromulina freiburgensis* Dofl (*After Doflein*, 1923)

of a wall between the two newly formed plasma membranes, except for a small circular area that becomes the pore. In certain genera the cytoplasm external to the statospore wall migrates inward through the pore and fuses with the cytoplasm within the wall, after which there is a formation of a plug that closes the pore.[3] In other genera there is a gradual disintegration of cytoplasm external to the wall as the statospore matures. Statospores of most genera are uninucleate, but those of one genus have been shown[4] to be binucleate.

When a statospore germinates, there is a dissolution of the plug or a separation of it from the spore wall (Fig. 100*F–H*). Most genera have an amoeboid migration of the protoplast from the enclosing wall and a formation of flagella during or after the migration,[5] but in certain genera[5]

[1] Cienkowski, 1870; Conrad, 1927, 1928; Doflein, 1923; Scherffel, 1911.
[2] Geitler, 1927 [3] Doflein, 1923 [4] Geitler, 1935*A*.
[5] Conrad, 1926; Hofeneder, 1913.

the protoplast within a wall divides to form two or four zoospores before the contents are liberated.

Evolution within the Chrysophyceae. The Chrysophyceae are a series with a large number of flagellated genera and relatively few genera with a truly algal type of organization. However, a sufficient number of immobile forms are known to show that evolution within the Chrysophyceae has paralleled that found in Chlorophyceae and Xanthophyceae.[1] The palmelloid type (the Chrysocapsales) is represented by about 10 genera and the filamentous type (the Chrysotrichales) by about 5. The chlorococcine type (Chrysosphaerales) include some four genera. Thus far, no siphonaceous forms have been found, and it is rather doubtful whether such forms exist because multinucleate chlorococcine forms, the potential ancestors of a truly siphonaceous plant, are also unknown.

The Chrysophyceae are richer than other algae in genera that have started evolving toward an animal-like rather than a plant-like organization. There are several genera in which the amoeboid cell is the dominant phase in the life history, and where autotrophic nutrition is supplemented by a mass ingestion of solid foods.[2] Some of the amoeboid genera[3] have evolved a true plasmodial organization.

Classification. The Xanthophyceae and Chlorophyceae each have, with a few exceptions, one basic type of flagellation in their motile cells and zooids. Chrysophyceae, on the other hand, have three different types of motile cell; the *chromulinad* type with one flagellum, the *ochromonad* type with two unequal flagella, and the *isochrysid* type with two equal flagella. Motile unicellular representatives of each of the three types seem to have been developed early in evolution of Chrysophyceae, and each of the three flagellar types has evolved, or started to evolve, into immobile multicellular algae.

A truly logical system of classification would necessitate the establishment of three subclasses, one for each type of motile cell, with the immobile genera assigned to the various subclasses according to the flagellation of their zooids. However, too few representatives of the coccoid and filamentous types are known to warrant such a system, and it is better, for the present, to follow Pascher's system[4] that divides the class into five orders.

ORDER 1. CHRYSOMONADALES

The Chrysomonadales (chrysomonads) include the genera in which the cells are motile during vegetative phases of the life cycle or in which amoeboid or rhizopodial stages are only temporary. Motile cells may be solitary or united in colonies of definite shape. The cells may be naked, or with an envelope that completely or incompletely surrounds the

[1] Pascher, 1914, 1925. [2] Pascher, 1915*A*, 1917.
[3] Pascher, 1916, 1916*A*. [4] Pascher, 1914, 1925, 1931.

protoplast. The protoplasts have typical golden-brown chromatophores. Many of the genera are known to produce statospores.

There are about 32 genera and 160 species, almost all of them fresh-water.

The order is divided into three suborders, each with a characteristic type of flagellation.

Suborder 1. Cromulineae

Members of the Chromulineae have cells with a single long flagellum. Some genera are unicellular, others have the cells united in colonies of definite form. The cells usually contain one or two chromatophores. Some genera have naked protoplasts. Others have the protoplast

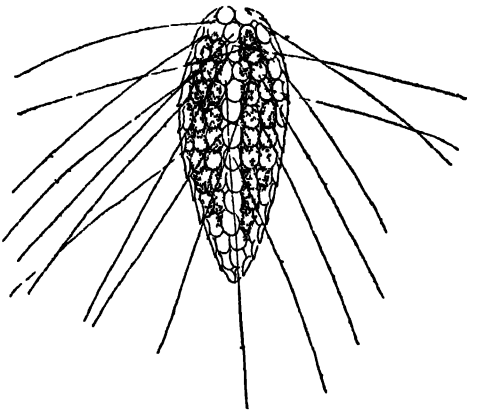


Fig 101 — *Mallomonas caudata* var *macrolepsis* Conrad (× 500)

surrounded by a closely fitting envelope with or without siliceous plates or surrounded by a lorica that stands free from it and is open at the upper end. Several genera are known to form statospores.

The suborder contains about 15 genera and 110 species. All but a few species are fresh-water.

Mallomonas, with some 55 species, is found in both fresh and brackish waters. Many of the fresh-water species are plankton organisms known only from clear-water lakes. The cells are solitary, free-swimming, and spherical, ellipsoidal, pyriform, or fusiform (Fig. 101). The protoplasts are enclosed by a thin pectic sheath containing many small overlapping siliceous scales. According to the species the scales are circular, elliptical, oval or polygonal; and transversely, diagonally, or irregularly arranged. In some species all scales and in other species only the terminal scales have a single long siliceous bristle excentrically inserted on the outer surface of the scale.[1] A majority of species have protoplasts containing

[1] Conrad, 1927; Iwanoff, 1900.

two chromatophores, but a few have only one chromatophore. Two species lack chromatophores.[1] The chief photosynthetic reserve is leucosin, and it generally accumulates in the posterior portion of a cell. The vacuolar system consists of a large noncontractile vacuole, which lies in the anterior part of a cell, and three to seven contractile vacuoles, which may be apical, medial, or basal in position. The single nucleus is quite large and with a conspicuous nucleolus. There is a large extranuclear granule (centrosome?) that connects with the base of the flagellum by means of a long rhizoplast.[1]

Reproduction is by longitudinal division and takes place while a cell is actively motile. The protoplast may also escape from the envelope and swim about as a naked zoospore. A zoospore swarms for a time; then it becomes immobile, spherical in shape, and surrounded by a gelatinous envelope. Similar palmelloid stages have been recorded[2] as developing from naked amoeboid protoplasts that have escaped from the sheath of surrounding siliceous scales.

Endoplasmic statospores have been described for several species.[3] They are usually spherical and without spines.

Suborder 2. Isochrysidineae

Genera referred to the Isochrysidineae have biflagellate cells, with the two flagella of equal length. The cells may be solitary or united in colonies of definite form.

The suborder contains about 7 genera and 16 species.

Synura, with some five species, is found in both fresh and brackish waters. It is widely distributed in fresh-water pools and lakes and sometimes is present in abundance. The cells are radiately united in spherical to oblong-ovoid colonies that are not surrounded by a gelatinous sheath (Fig. 102). The individual cells are obpyriform in shape. A cell is surrounded by a thin sheath of pectic material whose posterior end is prolonged into a hyaline stalk.[4] The distal end of a sheath is covered with spirally arranged siliceous scales bearing very short blunt spines.[5] The protoplast contains two laminate, curved chromatophores so placed that their concave faces are opposite. A protoplast contains a single centrally located nucleus and two or three contractile vacuoles near its base. Leucosin is the chief food reserve, and it collects in a single large granule toward the base of a cell. There is no eyespot. The two flagella at the anterior end of a cell are of equal length, but there are certain morphological and physiological differences between them.[6]

[1] Conrad, 1927. [2] Conrad, 1914, 1927. [3] Conrad, 1927, 1933.
[4] Conrad, 1926 [5] Korshikov, 1929; Petersen, 1918.
[6] Conrad, 1926; Petersen, 1918.

Cell division is always longitudinal. Ordinarily it merely increases the number of cells in a colony. Reproduction of many-celled colonies generally takes place by the cells grouping themselves radially about two centers, and the two parts then separating from each other. Failure of the daughter colonies to separate is probably the reason for the elongate colonies occasionally observed.[1] Reproduction may also be due to an amoeboid escape of a protoplast from its scale-covered sheath.[2] The liberated protoplast may remain amoeboid, or it may become a biflagellated zoospore. The zoospores swarm for a time and then develop into

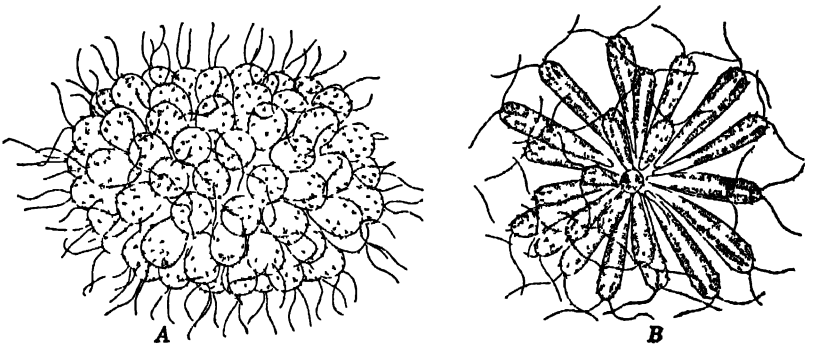


FIG. 102. *A*, *Synura uvella* Ehr. *B*, *S. Adamsii* G. M Smith. (× 400.)

Palmella stages or into new motile colonies. *Synura* may also form endoplasmic statospores.[3]

SUBORDER 3. OCHROMONADINEAE

The Ochromonadineae include all chrysomonads with two flagella of unequal length. The cells may be solitary or united in colonies.

There are about 11 genera and 45 species, most of which are freshwater.

Dinobryon, with about 20 species, is widespread in standing fresh waters. It often develops in abundance in the plankton of lakes. The cells are free-floating or sessile, and solitary or united in arborescent colonies (Fig. 103). Each cell is attached to the bottom of a conical, campanulate, or cylindrical lorica that has a closed pointed base and an open, cylindrical, or somewhat flaring apex. The lorica appears to be homogeneous, but treatment with proper reagents[4] shows that it is composed of successive segments, one nested within the other. A lorica may be hyaline or yellowish brown, and its surface may be smooth or spirally sculptured. It is said to contain cellulose[5] and to be somewhat impregnated with silica. The protoplast within a lorica is either spindle-shaped,

[1] Conrad, 1922. [2] Pascher, 1912. [3] Conrad, 1926.
[4] Pascher, 1921. [5] Lemmermann, 1900

conical, or ovoid and is attached to the base of the lorica by a short cytoplasmic stalk. Except for the basal stalk, the protoplast is rarely in lateral contact with the lorica.

The peripheral portion of the cytoplasm is quite firm and usually smooth, although sometimes finely granulate. The two flagella are borne at the anterior end of a protoplast; the longer extends for some distance beyond the open mouth of a lorica; the shorter rarely extends much beyond it. The protoplast contains one or more contractile vacuoles (apical, median, or basal in position) and either one or two

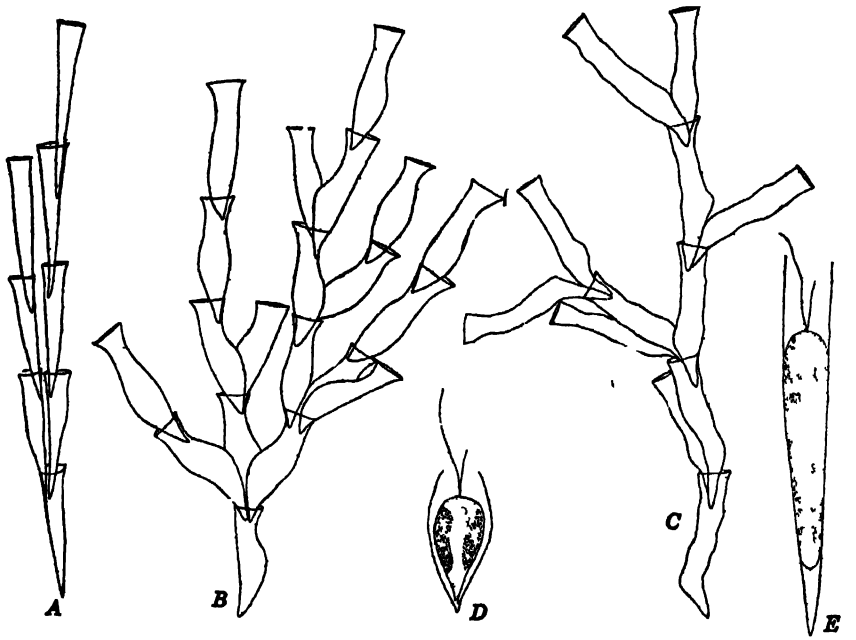


FIG 103 — *A*, *Dinobryon stipitatum* Stein *B*, *D. sertularia* Ehr. *C*, *D divergens* Imhof. *D*, *D Tabellariae* (Lemm.) Pascher *E*, *D calyciforme* Bachm. (*A–C*, × 400, *D–E*, × 1,000)

parietal laminate chromatophores (Fig. 103*D–E*). There is usually a conspicuous eyespot near the anterior end of a protoplast. The photosynthetic reserves accumulate chiefly as leucosin and in a single large granule toward the posterior end of a cell. The photosynthetic manufacture of foods may be supplemented by a mass ingestion of solid foods.

Reproduction is by longitudinal division of a protoplast into two daughter protoplasts. Unicellular species have one of the daughter protoplasts remaining within the old lorica; the other daughter protoplast becomes a free-swimming zoospore that eventually comes to rest and secretes a new lorica. Cells of colonial species may have one or both daughter protoplasts moving to the mouth of the old lorica and there

secreting new loricas.[1] Daughter protoplasts of colonial species may also become free-swimming zoospores or free-living amoeboid stages that eventually produce loricas.[2]

Several species of *Dinobryon* are also known to produce statospores. They are endoplasmic in origin but differ from statospores of other genera in that they are binucleate.[3] In many cases the statospores are perched upon the mouth of the old lorica instead of being contained within it.

The only reported case of gametic union among Chrysophyceae is in *D. sertularia* Ehr.[4] During the night the protoplast divides to form two daughter protoplasts, each of which becomes a biflagellate zoogamete. The zoogametes are liberated in the forenoon, and shortly afterward they fuse in pairs to form a zygote that soon loses its flagella and sinks to the bottom. Further development of the zygote is unknown.

ORDER 2. RHIZOCHRYSIDALES

The Rhizochrysidales include those Chrysophyceae in which the protoplast is amoeboid and in which flagellated stages, if formed, are only temporary. Unicellular genera may be naked or partially surrounded by a lorica. Colonial genera may be naked, or in dendroid colonies with each cell surrounded by a lorica. Reproduction may be solely by cell division or both by cell division and a formation of zoospores. Certain genera are known to form statospores.

There are about 12 genera and 20 species, all of them fresh-water in habit.

The Rhizochrysidales are Chrysophyceae in which the rhizopodial phase is dominant and not temporary. The chrysophycean nature of these organisms is evidenced by their golden-brown chromatophores, the types of food reserves, and in a few cases by their statospores. Some genera are colonial. In most of them colony formation is due to the cells' remaining connected by cytoplasmic strands after cell division,[5] but it may be due[6] to the formation of a fusion plasmodium.

Chrysamoeba, with the single species *C. radians* Klebs (Fig. 104), is a fresh-water unicellular genus without a lorica. In very rare cases a few cells may be temporarily united in colonies. For the greater part of the life cycle, the cell is in an amoeboid state with acutely pointed short pseudopodia radiating in all directions. The protoplast may contain either one[7] or two[8] golden-brown chromatophores that have or lack pyrenoids. Each cell contains a single large nucleus and, at times, a large granule of leucosin. Nutrition is in part photosynthetic and in part

[1] Klebs, 1892; Lemmermann, 1900. [2] Pascher, 1912. [3] Geitler, 1935*A*.
[4] Schiller, 1926. [5] Pascher, 1916. [6] Pascher, 1916*A*.
[7] Doflein, 1922; Penard, 1921. [8] Klebs, 1892.

by a mass ingestion of foods. The change from an amoeboid to a flagellated stage is accomplished by a retraction of the pseudopodia, a change to an ovoid shape, and the protrusion of a single long flagellum whose length is somewhat greater than that of a cell. During the motile phase, there is a contractile vacuole in the anterior end of a cell. The motile phase seems to last for a short time only,[1] after which the organism becomes more nearly spherical and develops denticulations that grow into pseudopodia. The flagellum may persist for some time after the cell has become amoeboid.

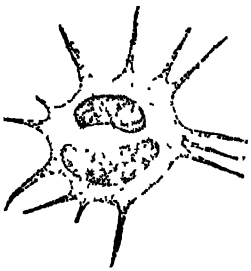


FIG. 104.—*Chrysamoeba radians* Klebs. (× 1,000.)

Thus far, cell division has been observed only when the organism is in an amoeboid condition. There is a mitotic division of the nucleus into two daughter nuclei and a constriction of the chromatophore into two parts.[2] Division of these organelles is followed by a pulling apart of the cell into halves, each with a chromatophore and a nucleus.

Statospores of *Chrysamoeba* are endoplasmic in origin.[2] Their walls are smooth and have a conspicuous collar and plug.

ORDER 3. CHRYSOCAPSALES

The Chrysocapsales have immobile vegetative cells united in palmelloid colonies by a common gelatinous matrix. Cell division may take place anywhere in a colony or may be restricted to one end of it. Cells of most, if not all, genera may be metamorphosed directly into a flagellated condition. Certain genera are known to form statospores.

The order includes about 10 genera and 14 species, all fresh-water.

Hydrurus, with the single species *H. foetidus* (Vill.) Kirchn., grows attached to rocks and stones in swiftly flowing cold-water streams. When conditions are favorable, the alga often covers the entire bottom of the stream. The plant body is greenish brown, of a tough gelatinous consistency, and 5 to 40 cm. in length (Fig. 105*A*). The basal portion is unbranched; the distal portion is divided into many branchlets arranged in dense tufts. Young plants and apices of branchlets of older plants have the cells uniseriately arranged within the gelatinous envelope.[3] Other portions of older plants are more than one cell in diameter (Fig. 105*B*). Here the majority of cells are ovoid, but they may be angular because of mutual compression. Each cell contains a single golden-brown chromatophore with a conspicuous pyrenoid.[4] The chromatophore usually lies on the side of the cell toward the thallus apex. The colorless portion of the protoplast contains granules of reserve food and five or six

[1] Penard, 1921. [2] Doflein, 1922.
[3] Klebs, 1892; Rostafiński, 1882. [4] Klebs, 1892; Lagerheim, 1888.

vacuoles.[1] The single nucleus lies next to the chromatophore. Division of the terminal cell of a branchlet is transverse, that of other cells may be vertical or transverse. Cell division may continue indefinitely, and an adult plant is composed of hundreds of thousands of cells.

It is very doubtful whether accidentally severed portions of a colony continue growth as independent plants for any length of time. Reproduction by means of zoospores is of frequent occurrence and usually takes place during the early morning hours. Zoospores are formed by a direct metamorphosis of recently divided cells near the tips of branchlets. They are tetrahedral in shape. One face bears a single long flagellum, and in the corner opposite this face there is a single large chromatophore (Fig. 105*C*). There are several contractile vacuoles in the cytoplasm next to the anterior face, but an eyespot is lacking.[2] When it stops swarming, a zoospore comes to rest with its anterior face downward, retracts its flagellum, assumes a spherical shape, and secretes a cylindrical gelatinous envelope. The first divisions of this germling are transverse (Fig. 105*D*).

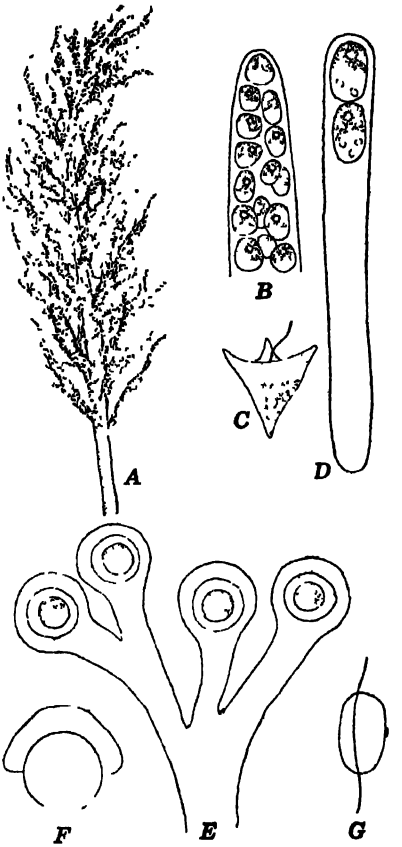


FIG. 105. - *Hydrurus foetidus* (Vill.) Kirchn. *A*, portion of a thallus. *B*, apex of a thallus *C*, zoospore. *D*, germling. *E*, statospores before liberation from thallus. *F G*, front and side view of a statospore. (*B–G, after Klebs*, 1892.)

Silicified statospores, with a fairly conspicuous plug and a wing-like ridge partially encircling the wall, are developed within cells borne in special gelatinous stalks protruding from the branchlets (Fig. 105*E G*). The stimulus causing a formation of statospores seems to be a rise in temperature of the water.[1]

ORDER 4. CHRYSOTRICHALES

The Chrysotrichales are to be distinguished from other Chrysophyceae by their branching filamentous thalli. The branches may be free from one another or compacted into a pseudoparenchymatous mass. Cell

[1] Klebs, 1892. [2] Klebs, 1892; Lagerheim, 1888.

structure, organization of the zoospores, and especially the typical chrysophycean statospores show that these algae belong to the Chrysophyceae.

There are five genera and seven species. One genus is found in brackish water, the others in fresh water.

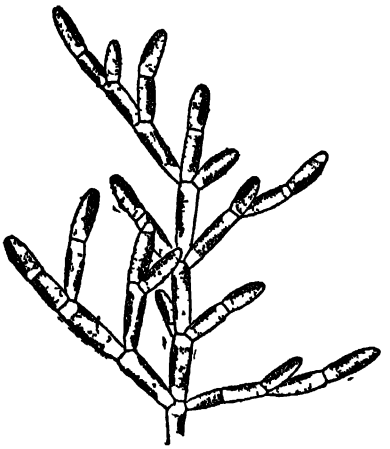


FIG. 106.—*Phaeothamnion confervicola* Lagerh. (× 485.)

Phaeothamnion, with three species, is a rare fresh-water alga that grows epiphytically upon other algae. Its thallus is composed of cylindrical to subovoid cells joined end to end in branched filaments with a conspicuous central axis and suberect lateral branchlets (Fig. 106). The basal cell of a thallus is hemispherical and attached to the substratum. The basal cell is usually without chromatophores; all other cells contain one, two, or several golden-brown chromatophores and store reserve foods mainly in the form of leucosin granules.[1] Palmelloid stages are of frequent occurrence. Palmelloid stages (Fig 107) are usually branched gelatinous tubes in which the cells are spherical and uniseriate in arrangement,[2] but the cells may be irregular in shape and irregularly distributed.[3]

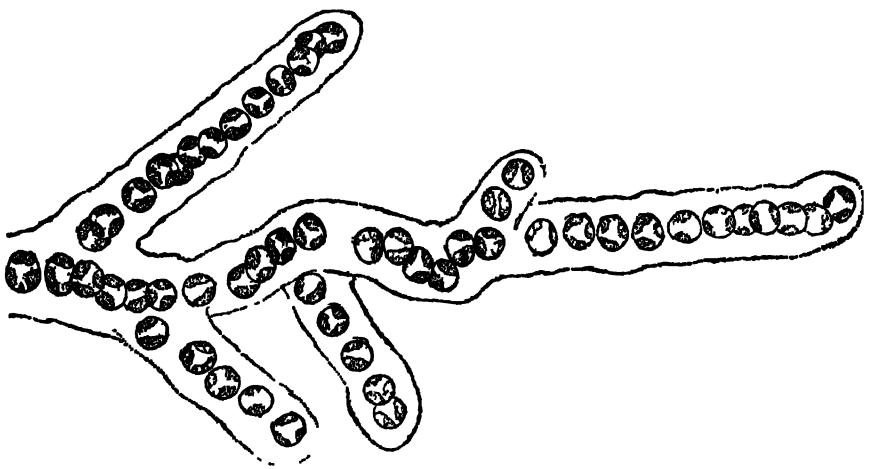


FIG. 107.—*Palmella* stage of a *Phaeothamnion* species [*P. Borzianum* Pascher (?)] (× 650.)

Reproduction is by the formation of one, two, four, or eight zoospores within a cell. They are liberated through a pore in the side of the parent-cell wall. The earlier descriptions[4] of structure of the zoospores are

[1] Lagerheim, 1884; Pascher, 1925. [2] Borzi, 1892; Pascher, 1925.
[3] Pascher, 1925. [4] Borzi, 1892; Lagerheim, 1884.

contradictory. A recent study of them[1] seems to show that they are biflagellate and have the two flagella quite different in length. Zoospores may also be formed while the alga is in a palmelloid condition.

Typical silicified statospores are also formed by *Phaeothamnion.*[2] Their development has not been studied in *Phaeothamnion* but those of another genus of the order have been shown[3] to be endoplasmic.

ORDER 5. CHRYSOSPHAERALES

The Chrysosphaerales are unicellular or nonfilamentous colonial Chrysophyceae in which the protoplast is not metamorphosed directly into a motile state.

There are about six genera and seven species.

The Chrysosphaerales correspond to the Chlorococcales of the Chlorophyceae and to the Heterococcales of Xanthophyceae. Cells of certain

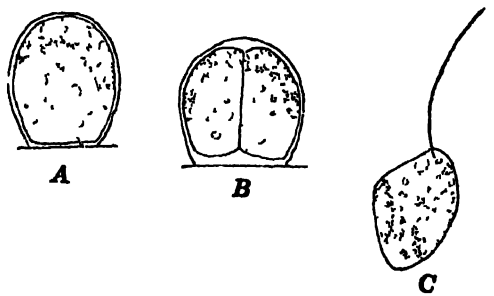


FIG. 108.—*Epichrysis paludosa* (Korshik) Pascher. (*After Pascher*, 1925*A*.)

Chrysosphaerales appear to be unable to divide vegetatively, but it is uncertain that, as in Chlorococcales, this is a universal character. None of the genera has been thoroughly investigated, and it is not improbable that certain genera now referred to the Chrysosphaerales will eventually be placed in the Chrysocapsales.

Epichrysis, with two species, has solitary or gregarious cells that grow epiphytically upon other fresh-water algae.[4] The cells are subspherical and somewhat flattened on the side toward the substratum (Fig. 108*A–B*). The protoplast contains a single large golden-brown chromatophore that lies toward the free side of the cell. The cytoplasm contains numerous small droplets of oil and small granules of leucosin.[1]

Multiplication may be due to a vertical bipartition of the protoplast and a secretion of a wall about each of the daughter protoplasts (autospores?) while they still lie within the parent-cell wall.[1] There may also be a formation[5] of uniflagellate zoospores (Fig. 108*C*). Zoospores

[1] Pascher, 1925. [2] Borzi, 1892; Pascher, 1925. [3] Geitler, 1927.
[4] Geitler, 1928; Meyer, K. I., 1930; Pascher, 1925.
[5] Meyer, K. I., 1930; Pascher, 1925.

that have ceased to swarm may come to rest upon a firm substratum and develop into typical vegetative cells, or they may be free-floating and develop into small palmelloid colonies. Cells of palmelloid colonies may produce either zoospores or statospores.[1]

CLASS 3. BACILLARIOPHYCEAE

The Bacillariophyceae (Bacillaricae), familiarly known as diatoms, have cells with one to many, variously shaped, yellowish to brownish chromatophores. Food reserves include both fats and an insoluble reserve (*volutin*), but there is never a storage of starch. Vegetative cells of all genera are nonflagellated and have a wall composed of overlapping halves. The wall consists of pectic materials more or less impregnated with silica. The cell wall has a characteristic ornamentation in which the markings are arranged in either a radially or a bilaterally symmetrical pattern.

Reproduction is usually by cell division into two daughter cells of slightly different size. There may be a formation of large rejuvenescent cells (auxospores) by direct enlargement of a protoplast or as a result of gametic union. The protoplast may also produce a statospore (endospore). Certain genera produce flagellated zooids that are probably gametic in nature.

There are about 170 genera and 5,300 species of diatoms,[2] some living, others known only in a fossil condition.

Distribution. Certain genera of living diatoms are found only in fresh waters, others only in salt water. Such genera as grow in both fresh and salt water usually have species that are strictly marine or strictly fresh-water. Most fresh-water diatoms are aquatics, and they may be sessile in habit, or free-floating. Many fresh-water diatoms develop in greatest abundance during spring or autumn months when the water is cool.

Some marine diatoms grow affixed to rocks or to algae, especially in the intertidal zone. Other marine species are strictly planktonic. Many marine plankton species are extremely sensitive to changes in temperature and salinity of the water. Their distribution is so limited that it is possible to follow the paths of ocean currents by determining the species of diatoms in the water. Marine plankton species, together with dinoflagellates, are of fundamental biological importance since all other life of the high seas is, in the last analysis, dependent upon them as a source of food.

Fossil Diatoms. Since the siliceous portion of a cell wall remains unaltered after death and decay of a cell, great numbers of empty walls accumulate at the bottom of any body of water in which diatoms live.

[1] Pacher, 1925. [2] Karsten, 1928.

Where conditions are exceptionally favorable and long continued, such accumulations may reach a considerable thickness. Deposits of fossil diatoms, known as *diatomaceous earth*, are found in various parts of the world.

Many different species are found in diatomaceous earth. Most of the fossil species are not older than the Cretaceous, and there is no satisfactory evidence showing that diatoms existed during the Palaeozoic.[1] Some genera are known only in the fossil condition, and certain others have more fossil than living species.

Some diatomaceous earths originated in fresh waters; others in the ocean. Fresh-water deposits consisting largely of plankton species were laid down in the beds of former lakes; those with nonplankton species predominating were not formed in lakes. All deposits of marine species are found inland and above the ocean as a result of geological changes. The best-known and most extensive deposits of marine species are those at Lompoc, California, where the beds are miles in extent and over 700 feet in thickness. The thickest deposits of diatomaceous earth thus far discovered are in the Santa Maria oil fields, California. Oil wells drilled in this region show, after correction for dip, that there is a subterranean deposit about 3,000 feet in thickness. The Lompoc deposit, like most others of marine origin, is composed almost exclusively of littoral species.

Diatomaceous earth is assuming an increasing importance as a commercial product, and the annual average production in this country for the years 1933 to 1935 was 244,342 tons.[2] The enormous quantity produced annually is more readily visualized when one realizes that a single ton has a volume of 50 to 260 cu. ft. Most of the diatomaceous earth comes from California, where the deposits are worked as open quarries. In quarrying, the overburden of soil is removed, and the diatomaceous earth is then quarried by means of hand picks, which split it into slabs that break apart in parallel cleavage planes. Power saws that cut the material into slabs *in situ* are also used.[3] Diatomaceous earth is also obtained from lakes in Florida by dredging with a suction pump and carrying the material through sluiceways to settling tanks. The material from some deposits can be utilized directly; that from other deposits must be incinerated to remove the organic substances present. Producers of diatomaceous earth market their product as powdered earth, calcined granules, manufactured brick, or sawn brick.

The industrial uses of diatomaceous earth are varied, and research is continually revealing new applications for this material. One of the first uses was as an absorbent for liquid nitroglycerin to make an explosive (dynamite) that could be transported with comparative safety. The inert medium used in the present-day manufacture of dynamite is wood

[1] Pia, 1927. [2] U. S. Bureau of Mines, 1936. [3] Calvert, 1930.

meal. Probably the most extensive industrial use of diatomaceous earth is in the filtration of liquids, especially those of sugar refineries. When a small amount of powdered diatomaceous earth is added to a sugar solution or other turbid liquid and the mixture forced through a filter press, the layer of diatomaceous earth deposited in the cloth screens out the suspended material present in the liquid. Another major use is in the insulation of boilers, blast furnaces, and other places where a high temperature is maintained. If the temperature is over 1000°F., diatomaceous earth is a much more efficient insulator than magnesia or asbestos, since it is much more resistant to shrinkage and does not fail at red heat. When used as an insulator, it is used in the form of bricks or as a loose powder between firebricks and an outer shell. The addition of but 1 or 2 per cent of diatomaceous material to cement greatly increases the workability of concrete and adds to its mechanical strength. The oldest commercial application is that of a very mild abrasive in metal polishes and tooth paste. This use is so well known that many people think that it is the major use of diatomaceous earth. The amount used for polishes is, however, very small as compared with that used for other purposes. The amount used in polishes has increased greatly in recent years with the use of diatomaceous dust as the base of polishes for cleaning automobiles finished in artificial lacquers.

The Cell Wall. Diatomologists have centered their attention on the structure of the wall, and their taxonomic treatment of the group is based upon wall structure and ornamentation. This intense specialization is largely responsible for the special terminology currently used to designate the various parts of a wall. Both the wall alone and the wall with its contained protoplast are called a *frustule.* The wall consists of overlapping halves that fit together as do the halves of a bacteriologist's Petri dish. The outer of the two half walls is an *epitheca* and the inner a *hypotheca.* The silicified portion of either consists of a more or less flattened *valve* whose flange-like margins are attached to a *connecting bank* or *cingulum.* The cingulum is usually firmly united to the valve, but in "cleaned" diatoms (those in which all organic material has been removed by oxidizing agents) and in diatomaceous earth one frequently sees connecting bands that have become separated from valves. A cingulum is an open instead of a closed hoop, and one with a gap between the approximated ends.[1] Some diatoms have additional connecting bands (intercalary bands), interpolated between epitheca and hypotheca, and there may be one, two, or more of them. When a frustule lies so that the valve side is uppermost, it is said to be in *valve view;* when the cingulum is uppermost, it is in *girdle view.* According to the genus, a

[1] Palmer and Keeley, 1900.

water mount will show practically all individuals in valve view, practically all in girdle view, or indiscriminately in valve and girdle views.

Both half walls of a frustule consist of an organic matrix composed in large part of pectin [1] The wall gives no reaction for either cellulose or callose. The watery gelatinous sheath surrounding many plankton species is probably pectic acid [2] The valve and cingulum portions of a half wall are silicified Some[3] think that silicification is not a simple impregnation with silica but a chemical combination of silicon with the

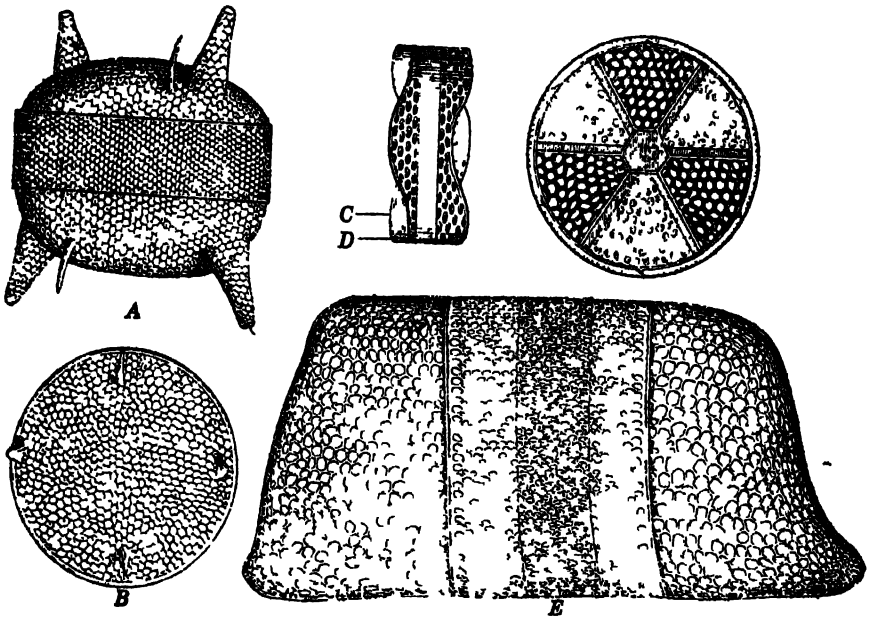


FIG 109 —Centric diatoms *A–B* girdle and valve views of *Biddulphia Smithii* (Rab) V H *C–D* girdle and valve views of *Actinoptychus undulatus* Ralfs *E*, girdle view of *Isthmia enervis* Ehr (*From Schutt*, 1896)

organic material of a wall Others[4] hold that there is no organic material in the silicified portion of a wall Silicification may be demonstrated by incineration, by decay, or by treatment with chromic acid, potassium chlorate, or other oxidizing agents Siliceous material may be removed from a wall by treating frustules with hydrofluoric acid, which affects neither the pectic wall material nor the protoplast. The amount of silicification is quite variable It is often so scanty in plankton species that the frustules cannot be "cleaned" by the usual methods. Non-plankton species usually have highly silicified walls The extent to which the wall is silicified is in part dependent upon the amount of available

[1] Liebisch, 1928; Mangin, 1908 [2] Schroder, 1902
[3] Mangin, 1908 [4] Liebisch, 1928, 1929

siliceous materials in the water, and it has been shown[1] that aluminum silicate is the chief compound used in silicification. An abundance of available silicates seems to stimulate the formation of new cells, and a close correlation has been demonstrated[2] between flood waters with a high proportion of dissolved silicates and a local increase in the number of diatoms. Cultural studies have shown that certain diatoms cannot form new cells if silicon is not available,[3] and that other species may

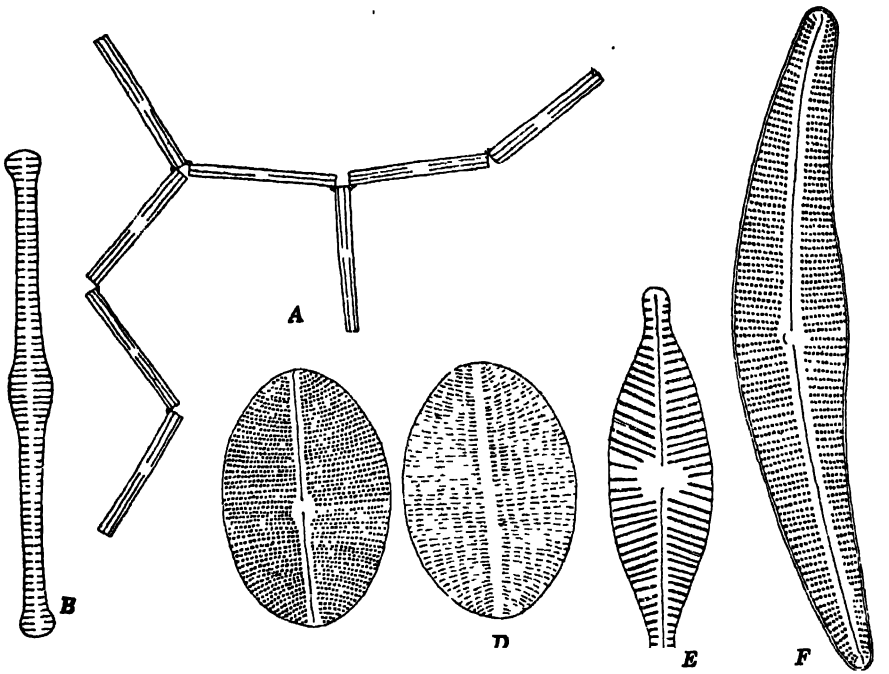


FIG. 110.—Pennate diatoms. *A–B*, girdle and valve views of *Tabellaria fenestrata* (Lyngb.) Kütz. *C–D*, the two dissimilar valves of a cell of *Cocconeis Pediculus* Ehr. *C*, epitheca. *D*, hypotheca. *E*, *Navicula rhyncocephala* Kütz. *F*, *Cymbella lanceolata* (Ehr.) Brun. (*A*, × 400; *B*, × 1,000; *C–E*, × 1,300; *F*, × 650.)

continue division through many cell generations when grown in a medium lacking available silicates.[4]

The siliceous material deposited in a valve is not laid down as a smooth sheet. Instead, the sheet is areolate or striate and has the areolae or striae in patterns that are characteristic for the genus and species. The ornamentation of a valve is according to one of two general patterns. In the *centric diatoms* (*Centrales*, Fig. 109) it is radially symmetrical about a central point; in the *pennate diatoms* (*Pennales*, Fig. 110) it is bilaterally symmetrical or asymmetrical with respect to an axial strip.

[1] Coupin, 1922. [2] Pearsall, 1923.
[3] Bachrach, 1927. [4] Bachrach and Lefèvre, 1929.

Some species, especially those of marine Centrales, have very coarse markings; certain Pennales have punctae or striae so fine that they are only revealed by the best microscopes.

The coarse markings of many marine centric diatoms are due to thinner places (areolae) in the siliceous deposit. The areolae are generally bounded by ridges that lie on the inner or the outer face of the valve (Fig. 111*A–B*). Areolae may have minute vertical canals (pores) running through them or incomplete canals (poroids), which do not entirely perforate the wall.[1] Pores vary in size from 0.1 to 0.6μ.

The ornamentation of pennate diatoms is due to thin places, not perforations, in the wall. A few Pennales have valves with one or more true perforations (Fig. 111*C–D*) that are either median or polar.[2] The thin places (*punctae*) lie in rows bilaterally disposed with respect to a

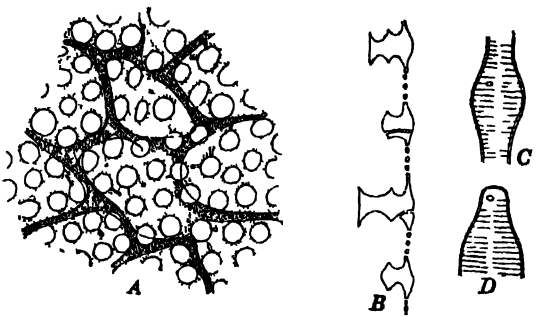


FIG 111.—*A B*, surface view and cross section of a portion of the wall of *Isthmia nervosa* Kutz. *C*, median mucilage pore of *Fragilaria virescens* Ralfs *D*, terminal mucilage pore of *Tabellaria fenestrata* Kutz. (*A–B, after Muller*, 1898, *C–D, after Muller*, 1899.)

longitudinal strip (the *axial field*) running the length of a valve. In many cases the rows of punctae are so minute and so close together that they appear to be striae (Fig. 110*A*). The axial field usually coincides with the longitudinal axis of a valve but may be asymmetrical with respect to it. An axial field may be homogeneous in structure or it may be perforated by a longitudinal slot, the *raphe*. An axial field without a longitudinal slot is a *pseudoraphe*. Axial fields of the two valves of a frustule are usually alike, but there are certain genera in which one valve has a raphe and the other a pseudoraphe (Fig. 110*C–D*).

A raphe is usually interrupted midway between its ends by a thickening of the wall (the *central nodule*), and there are often similar swellings (*polar nodules*) at either end of it. The raphe is not a simple cleft in the wall. Instead, it is an extremely complicated structure, and that of *Pinnularia* may be cited as fairly typical. As seen in valve view, the raphe of *Pinnularia* is a sigmoid line that runs from one polar nodule to the central nodule and thence to the other polar nodule (Fig. 112*B*).

[1] Muller, 1898, 1899, 1900, 1901. [2] Gemeinhardt, 1926; Müller, 1899.

As seen in vertical transverse section it is >-shaped and not a vertical slot.[1] The upper arm of the > is called the *outer fissure* and the lower arm the *inner fissure.* Near the vicinity of each polar nodule the outer fissure bends in a semicircle and terminates in a linear expansion called the *polar cleft.* In the same region the inner fissure bends in the opposite direction and terminates in a *funnel cleft* that opens on the inner face of the cell wall. The central nodule is a conical projection toward

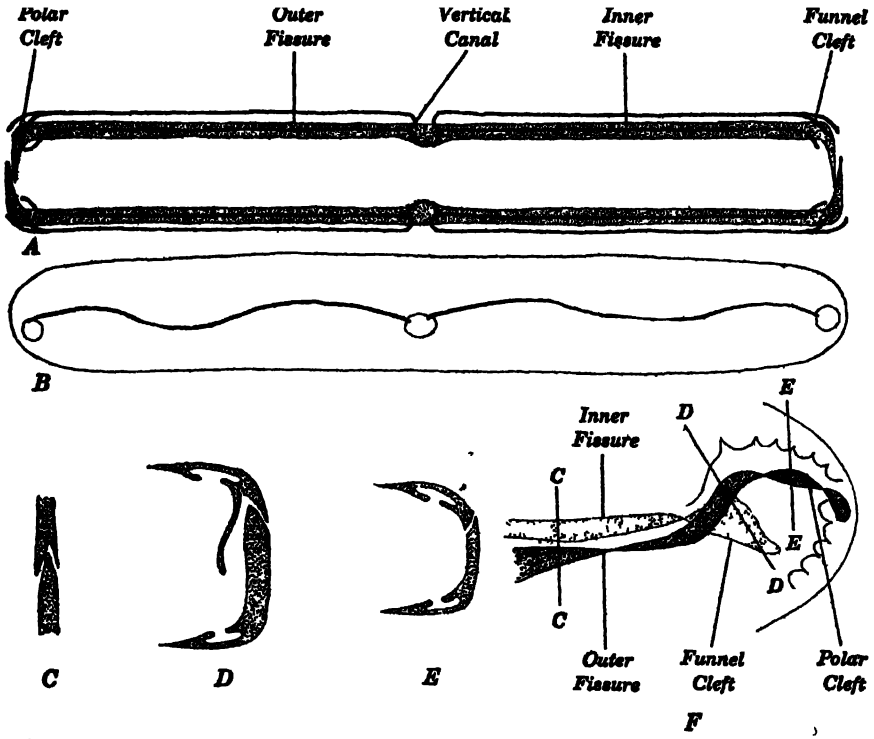


FIG. 112.—Structure of the raphe of *Pinnularia.* *A*, vertical longitudinal section of a frustule. *B*, surface view of a valve. *C*, vertical section of a valve wall cut in the plane *CC* of Fig *F* *D*, a similar section cut at *DD*. *E*, a similar section cut at *EE*. *F*, terminal portion of a valve showing the inner and outer fissures in surface view. (*A–B, modified from Müller*, 1889; *C–F, after Müller*, 1896.)

the interior of the cell, and in this region the outer and inner fissures in each half of a valve are connected with each other by vertical canals. Inner fissures of the anterior and posterior parts of a valve are also connected with each other by a horizontal canal running through the inner face of the central nodule.

Structure of the Protoplast. Immediately within the cell wall is a fairly thick layer of cytoplasm in which the chromatophore or chromatophores are imbedded. Internal to the cytoplasmic layer is a con-

[1] Müller, 1889, 1896.

spicuous central vacuole. Pennate diatoms often have the central portion of the vacuole transversely interrupted by a broad band of cytoplasm in which lies a spherical or ovoid nucleus.* The chromatophores vary in shape and number from species to species. The structure of chromatophores is quite constant for some genera and variable for others. For this reason systems of classification based largely upon the chromatophores are unsatisfactory. Protoplasts of Centrales usually contain many discoid or irregularly shaped chromatophores. Those of Pennales usually contain two chromatophores or a single irregularly lobed and perforated chromatophore (Fig 113). If two chromatophores

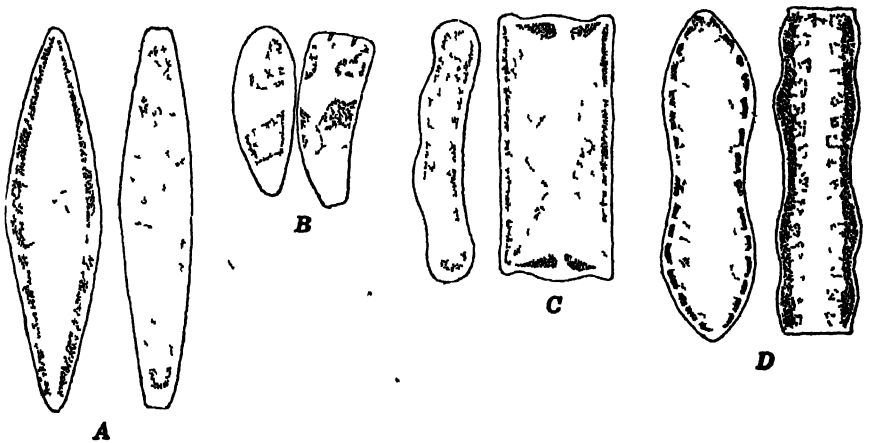


FIG 113.—Valve and girdle views of the chromatophores of various diatoms. *A*, *Navicula radiosa* Kutz *B*, *Rhoicosphenia curvata* (Kutz.) Grun *C*, *Eunotia diodon* Ehr. *D*, *Cymatopleura solea* f. *interrupta* (*After Ott*, 1900.)

are present, they are laminate and extend longitudinally along opposite sides of the protoplast.[1] Chromatophores may contain one to several pyrenoids or may lack them entirely. Pyrenoids are usually ovoid, biconvex, or planoconvex in shape. Sometimes they lie in a bulge at the inner face of, or entirely separated from, the chromatophore.[2] Pyrenoids of diatoms are of the naked type (that is, devoid of a starch sheath) and their exact role in the metabolism of a cell is uncertain. Possibly they function as elaioplasts and are concerned in the formation of oils.

Typically the chromatophores are of a rich golden-brown color, but a few species have chromatophores that are a vivid green or even a bright blue.[3] Colorless diatoms in which there are no chromatophores have also been recorded.[4] The nutrition of colorless diatoms is saphrophytic.[5] The golden-brown color of chromatophores has been ascribed to *diatomin*, a special pigment which masks the chlorophyll and asso-

[1] Heinzerling, 1908; Ott, 1900. [2] Mereschkowsky, 1903.
[3] Molisch, 1903. [4] Benecke, 1900. [5] Richter, 1909.

ciated yellow pigments. The evidence for and against the presence of diatomin is quite contradictory, but those who argue that there are no pigments other than chlorophyll and carotinoids[1] seem to have the better of those who maintain[2] that there is a special pigment.

Fats are the chief food reserve formed as a result of photosynthetic activity. These accumulate in droplets, often of considerable size, either in the cytoplasm or in the chromatophores. The method by which fats are formed is unknown, but the fact that they serve as food reserves is demonstrated by their gradual disappearance when cells are kept continuously in a dark room. There are other food reserves in addition to fats. The insoluble food granules in the protoplast have been called volutin[3] and have been thought[4] to be rich in nucleic acids. The microchemical methods by which the nucleic acids were demonstrated were extremely crude, and one may just as well identify volutin with the leucosin found in Xanthophyceae and Chrysophyceae. The paired plates sometimes seen in the cytoplasm immediately outside of a nucleus[5] are probably structures concerned in the development of a mitotic spindle and not food reserves.

Diatom cells are uninucleate, and the nucleus is spherical to biconvex in shape. In centric species it lies imbedded in the cytoplasm next to the wall; in most pennate species it lies in a cytoplasmic bridge across the middle of a protoplast. Numerous cytological investigations have shown that the nucleus has a definite membrane, one or more nucleoli, and a chromatin-linin network in the intervening space between the two. Some species have a centrosome lying at one side of, or in a peripheral depression of, the nucleus; other species lack a centrosome.[5] Nuclear division is always mitotic and generally with the formation of a considerable number of chromosomes. Nuclei of vegetative cells of all pennate diatoms are diploid. Those of certain centric species also seem to be diploid, and the same may possibly be true of all centric species.

Locomotion of Diatoms. Many of the free-living, and some of the colonial, pennate diatoms have the ability to move spontaneously. None of the centric diatoms moves independently. Movement is generally by a series of jerks and always in the direction of the long axis of the cell. After a cell has moved forward for a short distance, it pauses for an instant and then, with the same jerky motion, moves backward along nearly the same path. Sometimes the movement is smooth instead of jerky, but there is always a forward and backward progression.

Numerous theories have been advanced to account for the motility of diatoms, but Müller's theory of cytoplasmic streaming[6] is now almost

[1] Kohl, 1906. [2] Molisch, 1905. [3] Meyer, A., 1904.
[4] Guilliermond, 1910. [5] Lauterborn, 1896.
[6] Müller, 1889, 1893, 1894, 1896, 1897, 1908, 1909.

universally accepted as explaining the locomotion of Bacillariophyceae. The intimate connection between movement and the presence of a raphe was brought out very clearly when it was shown that motility is restricted to those pennate species that have a true raphe.[1] Müller's theory of cytoplasmic cyclosis was based upon studies on *Pinnularia*.[2] He holds that a stream of cytoplasm flows along the free face of the outer fissure in each of the half cells. Beginning at the anterior polar cleft (page 202) of the outer fissure, the stream moves backward along the outer fissure until it reaches the central nodule, where it moves vertically inward through the anterior vertical canal of the central nodule (Fig. 114). Coincident with this streaming, there is an outward flow of cytoplasm in the posterior vertical canal of the central nodule, and this stream moves backward along the outer fissure to the polar cleft in the posterior

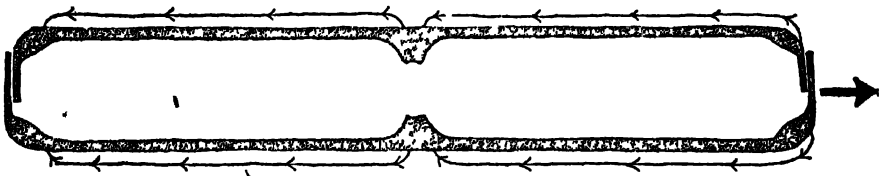


FIG. 114.—Diagram of the streaming of cytoplasm on the outer face of a *Pinnularia* frustule. The heavy arrow indicates the direction of movement of the frustule. (*Modified from Muller*, 1893.)

polar nodule. Movement of cytoplasm in the outer fissures is accompanied by a compensatory flow in the inner fissures that travels in the opposite direction.

Propulsion of a frustule is in a direction opposite to that of cytoplasmic streaming in the outer fissures. Propulsion is due to frictional water currents set up by the flowing cytoplasm and to cyclonic currents in the region of the polar nodules. Cytoplasmic cyclosis was first demonstrated by the behavior of the suspended particles when cells were mounted in dilute India ink. Girdle views of cells mounted in such suspensions show that there is a linear flow of particles from anterior polar nodule to central nodule, a whirlpool of particles in the region of the central nodule, and a linear flow of particles from central nodule to the posterior polar nodule.

Cell Division. When a diatom cell divides, there is generally a formation of two daughter cells of slightly different size. Most cells divide during the midnight hours, but some[3] divide between 7 and 8:30 A.M. The first indication of division is an expansion of the protoplast that causes a slight separation of the two overlapping half walls. This is followed by a mitotic division of the nucleus in a plane perpendicular to the valves (Fig. 115*A*). Nuclear division of pennate diatoms is

[1] Muller, 1889. [2] Müller, 1889, 1893, 1896. [3] Gemeinhardt, 1925.

generally accompanied by a division of the chromatophores. If a cell has a single chromatophore, its division is always longitudinal; if there are two chromatophores, their division may be longitudinal or transverse.[1] Species with numerous chromatophores do not have a bipartition of them until after the daughter cells have been formed. Pyrenoids, at least in chromatophores with conspicuous ones, increase in number by division and not by formation *de novo*.[2] Duplication of cell organs is followed by a longitudinal bipartition of the protoplast in a plane parallel to the valves (Fig. 115*A–B*). One of the daughter protoplasts lies within the epitheca of the parent-cell wall and the other within the hypotheca (Fig. 115*D*). Each daughter protoplast soon secretes a new half wall next its girdle and free face. The newly formed half wall is always the hypotheca of a daughter frustule, and the old

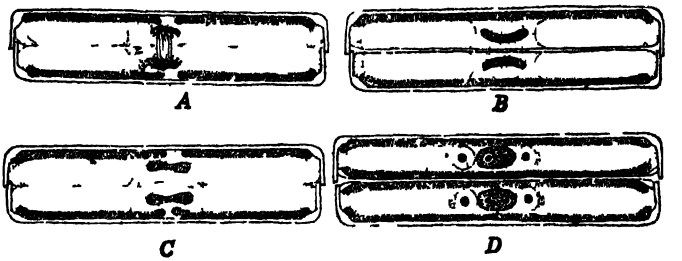


FIG 115.—Four stages in the cell division of *Navicula oblonga* Kutz. (*After Lauterborn, 1896.*)

half wall received from the parent cell, irrespective of whether it was formerly an epitheca or a hypotheca, is always the epitheca. It follows, therefore, that in a population descended from a single cell, half of the cells have an epitheca that was secreted in the previous cell generation, a quarter of them an epitheca that was secreted two cell generations back, an eighth of them an epitheca secreted three generations back, and so on until there are two cells, each with an epitheca derived from the original cell.

Utilization of the two old half walls as epithecae for the daughter cells results in one cell being the same size as the parent and the other being slightly smaller. Continuation of this through several cell generations would result in a population with some cells appreciably smaller than others, but a population in which some cells are of approximately the same size as the original parent (Fig. 116). This progressive diminution in size of certain cells, sometimes known as Pfitzer's law,[3] does not always obtain because the girdle of an epitheca may be so elastic that the new hypotheca of a frustule is the same size, or larger, than the

[1] Ott, 1900. [2] Heinzerling, 1908. [3] Pfitzer, 1871, 1882.

old half-cell wall. Daughter cells may also become longer than the parent cell as a result of "secondary growth"[1].

When cells become progressively smaller, the diminution in size may be in all planes or only in one axis of the valve face.[2] Progressive diminution in size is not accompanied by a corresponding reduction in fineness of the ornamentation.

The best evidence for or against Pfitzer's law has been found in pure cultures started from a single cell. In certain species there is no appreciable diminution in size even when the cells are carried through innumerable cell generations.[3] Other species grown in pure culture behave in accordance with Pfitzer's law and show[4] a progressive decrease in size

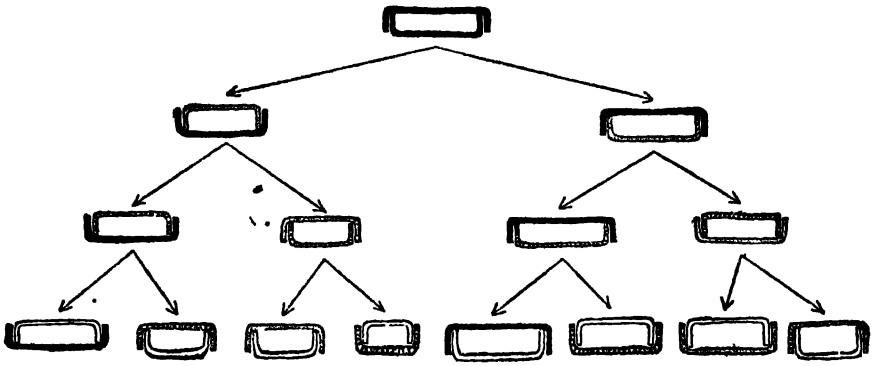


FIG 116.—Diagram showing progressive diminution in size of certain frustules through successive cell generations of a diatom. Half walls of the first generation are in black, those of the second generation are in stipple, those of the third generation are in cross-hatched stipple, and those of the fourth generation are unshaded

of certain cells. Statistical studies on cell size of diatoms growing under natural conditions[5] show that they also may or may not become progressively smaller. Diminution in size does not continue indefinitely, because cells of any particular species are unable to divide further when they reach a certain minimal size. These cells die off because they can neither divide nor form rejuvenescent cells (auxospores) of a much larger size.[6]

Pennate diatoms occasionally have the protoplast forming several successive sets of new half walls without escaping from the original wall surrounding a cell. Successively formed half walls, which are progressively smaller, nest one within the other, and the later-formed walls often have imperfectly developed raphes. Such *craticular stages* are immobile. Craticular stages result from unfavorable environmental

[1] Gemeinhardt, 1927. [2] Torka, 1928; Geitler, 1932.
[3] Allen and Nelson, 1910; Richter, 1909. [4] Geitler, 1932; Meinhold, 1911.
[5] Geitler, 1932; Bethge, 1935. [6] Geitler, 1932.

conditions, especially an increase in salt content of the water.[1] Return of favorable conditions induces active cell division in a craticular stage, and within a cell generation or two the daughter cells are normal in structure and migrate from the nested half walls of the parent cell.

Statospores. Thick-walled resting spores (variously called statosphores, endospores, or cysts) may be formed within the frustules of centric diatoms. They are best known in marine plankton species but have also been found in three fresh-water plankton genera. Statospores are enveloped by a wall with two overlapping halves, but the shape and ornamentation of a statospore wall differs from that of a vegetative cell (Fig. 117). In most cases the epitheca of a statospore is ornamented with spines and the hypotheca is smooth.[2] The protoplast of a vegetative cell contracts at the time of statospore formation, but the details of spore formation are unknown. There is a strong probability that they are formed in the same endoplasmic manner as are the homologous spores of Chrysophyceae and Xanthophyceae.

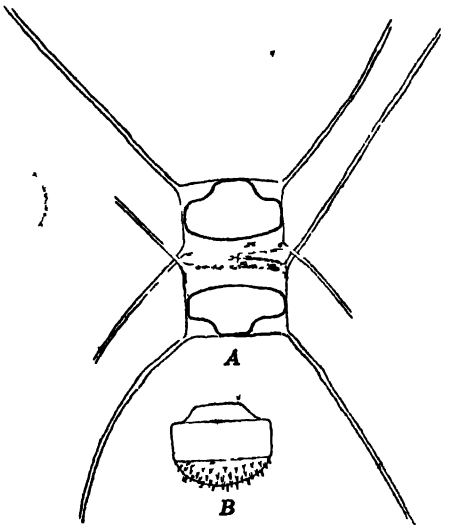


FIG. 117.—Statospores of *Chaetoceros Elmorei* Boyer. *A*, two frustules, each containing an immature statospore. *B*, a mature statospore. (*After Boyer*, 1914.)

The thick-walled spores formed in pairs or in greater numbers[4] within frustules of a few centric and pennate diatoms are probably different from true statospores. These resting spores, whose germination has not been observed, seem to be formed at the end of the vegetative season[5] and may possibly tide the diatom over unfavorable seasons. However, resting spores are not necessary to carry fresh-water diatoms through unfavorable seasons since vegetative cells of many species may withstand desiccation for months and years.

Auxospores of Pennate Diatoms. Many pennate diatoms form rejuvenescent cells (auxospores) considerably larger than the vegetative cells producing them. Auxospore formation by pennate diatoms is always associated with sexual reproduction and due either to enlargement of a zygote or to enlargement of a parthenogenetic gamete. Auxospore formation takes place in cells that have become progressively

[1] Geitler, 1927*D*; Liebisch, 1929. [2] Boyer, 1914; Mangin, 1912; Schütt, 1896.
[3] Hustedt, 1927–1930. [4] West, 1912. [5] West, 1916.

smaller but before they have reached the minimal size.[1] Production of auxospores is also correlated with environmental conditions and their formation may be induced by transferring vegetative cells to a weaker concentration of the culture medium.

There are four general methods[2] by which Pennales produce auxospores: (1) two cells each produce two gametes which fuse in pairs to form two zygotes (auxospores); (2) two cells each produce a single gamete, and the two fuse to form a single zygote (auxospore); (3) a single cell may produce two gametes that unite with each other to form a zygote (auxospore), or a cell may produce two gamete nuclei that unite to form a zygote nucleus; and (4) a single cell produces a single gamete which develops parthenogenetically into an auxospore.

Irrespective of the manner of formation, there is an immediate elongation of the auxospore, or auxospores, to considerably more than the length of the parent cell or cells. The elongation may be in a plane parallel with or at right angles to the old empty parent half walls. Completion of elongation is followed by a formation of a silicified wall whose epitheca and hypotheca have an ornamentation much like that of the parent cell. The mature auxospore germinates immediately by dividing longitudinally into two daughter cells, both of which soon divide and redivide. Vegetative cells formed by division of an auxospore are approximately the same length as the auxospore, that is, of approximately the maximal length and breadth for the particular species. Division of the auxospore (zygote) nucleus is equational, and all subsequent nuclear divisions preceding vegetative cell division are also equational. Because of this all vegetative cells of Pennales are diploid.

In auxospore formation, according to the first general method, the pair of cells may be sister cells or two that are not derived from a common parent cell. In either case they lie within a common gelatinous envelope. Several species have been studied cytologically and all of them have been shown[3] to have a reductional division of their nuclei prior to gamete formation. Conjugating cells of several other species have been shown to produce four nuclei in a cell before the protoplast divides to form two gametes, each with a single nucleus or with a functional and a degenerating nucleus. The inference is that nuclear division in these cells is also reductional, but the actual halving of the chromosome numbers has not been demonstrated. All species producing pairs of auxospores have protoplasts of both cells dividing to form two gametes (Fig. 118). Division of a protoplast may be transverse[4] or longitudinal,[5] and the two gametes may be of equal or unequal size. Gametes of

[1] Geitler, 1932, 1935. [2] Geitler, 1935.
[3] Von Cholnoky, 1927, 1928, 1929, 1933; Geitler, 1927*C*, 1928*A*; Meyer, K., 1929.
[4] Karsten, 1896, 1897; Klebahn, 1896. [5] Geitler, 1927*B*, 1928*A*.

unequal size may be due to an unequal division of the parent protoplast[1] or to an enlargement of one gamete shortly after it is formed.[2] Even when two gametes are morphologically similar, there may be such physiological differences as one being mobile and the other passive. Movement of gametes is always amoeboid and is never due to flagella. Two gametes formed within a cell always unite with those in the other cell of an apposed pair and never with each other. Fusion of gametes usually takes place midway between the parent frustules, but a gamete

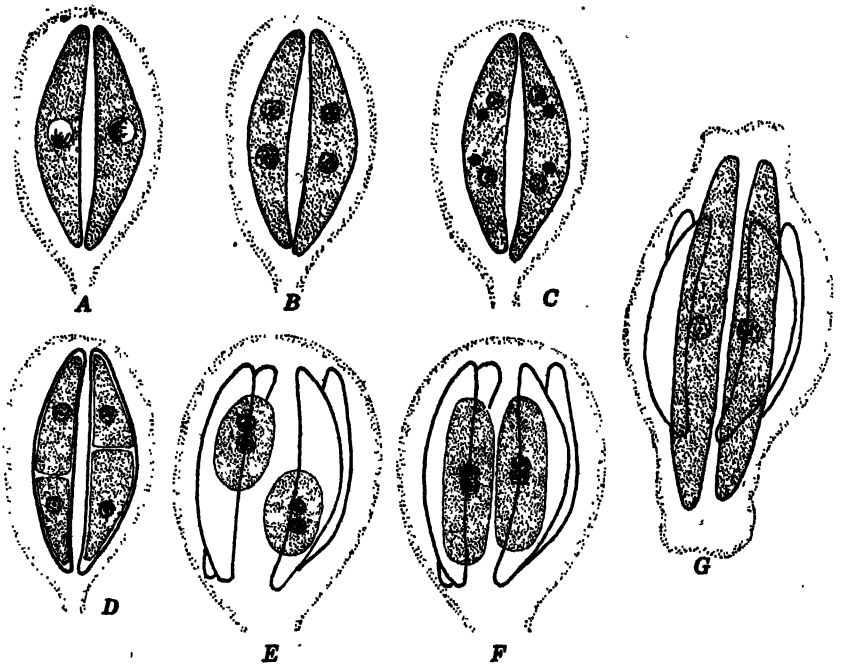


FIG. 118.—Diagrams showing the formation of two auxospores by two conjugating cells of a pennate diatom, *Cymbella lanceolata* (Ehr.) Brun. *A–C*, reduction division and degeneration of two nuclei in each frustule. *D*, after the division of each protoplast into two gametes of unequal size. *E*, young zygotes. *F–G*, elongation of the zygotes to form auxospores. (*Diagrams based upon Geitler*, 1927*B*.)

from one frustule may migrate to and unite with a gamete in the other frustule.[3] In the latter case there is a simultaneous or subsequent migration of a gamete from the second frustule and a union of it with the gamete remaining in the first frustule. Gametic union is soon followed by a fusion of the gamete nuclei and an elongation of the zygote into an auxospore.

Several species with two cells producing a single auxospore have also been shown[4] to have a reduction division of nuclei in the conjugating

[1] Geitler, 1927*B*. [2] Karsten, 1896. [3] Geitler, 1927*B*, 1928*A*.
[4] Von Cholnoky, 1927; Geitler, 1927*A*; Karsten, 1912.

cells. In some species there is a formation of four nuclei followed by a disintegration of three of them;[1] in other species one of the daughter nuclei of the first division begins to degenerate as soon as it is formed[2] and the other nucleus divides into two daughter nuclei, one of which disintegrates (Fig. 119) In either case, the two protoplasts with a single haploid nucleus become amoeboid gametes that meet midway between the old empty frustules and there unite to form a zygote.

The sexual production of a single auxospore by a single cell has been described for several species, but in none of them is it established

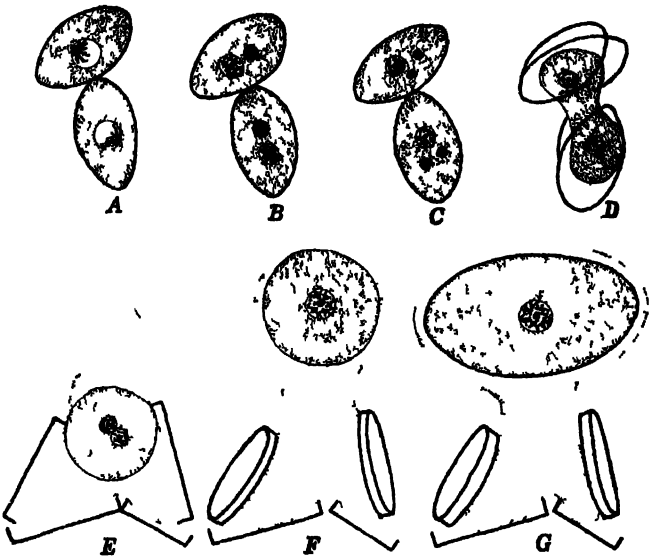


FIG 119 —Diagrams showing the formation of one auxospore by the conjugation of two cells of a pennate diatom *Cocconeis placentula* var *Klinoraphis* Geitler *A C*, reduction division and degeneration of all but one nucleus in each frustule *D* gametic union *E*, young zygote *F G*, enlargement of the zygote to form an auxospore (*Diagrams based upon Geitler*, 1927*A*)

beyond all doubt. *Amphora Normani* Rab. is a species with a single chromatophore Auxospore formation in[3] solitary cells of this species begins with a contraction of the protoplast A contracted protoplast contains two nuclei and two chromatophores There then follows a springing apart of the two half walls and an elongation of the protoplast to form an auxospore more than twice as long as the original cell. Early stages in elongation of an auxospore are binucleate; older stages are uninucleate but sometimes with two nucleoli in the nucleus. It has been held[4] that nuclear division producing the binucleate condition is reductional and that the fusion of two sister haploid nuclei produces a single diploid nucleus in the auxospore.

[1] Karsten, 1912. [2] Geitler, 1927*A*
[3] Geitler, 1928*B*. [4] Geitler, 1928*B*, 1932

Parthenogenetic development of an auxospore from a single gamete seems definitely established in *Cocconeis placentula* var. *lineata* (Ehr.) Cleve Here[1] two cells lie within a common envelope but give rise to auxospores without gametic union (Fig 120). The nucleus in each cell goes into a synapsis-like contraction and then into a "diakinesis" that produces about 28 single chromosomes instead of pairs of chromosomes There then follows the usual double division, with one nucleus degenerating after the first division and one disintegrating after the second division The result is a uninucleate cell in which the protoplast is a gamete with a diploid instead of a haploid number of chromosomes. The gamete with a diploid nucleus then develops directly into an auxospore

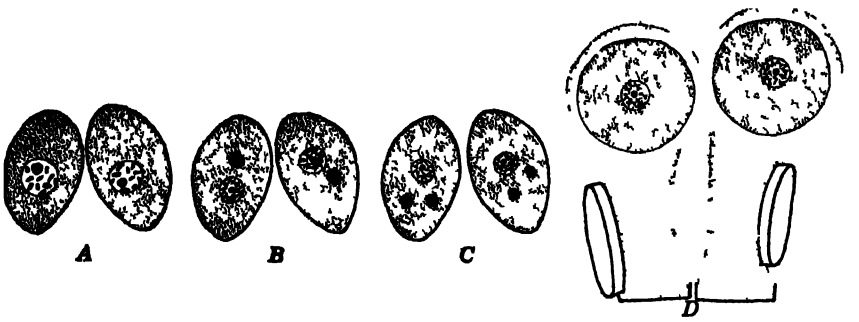


FIG 120.—Diagrams showing the parthenogenetic development of auxospores in each of two "conjugated" cells of a pennate diatom *Cocconeis placentula* var *lineata* (Ehr) Cleve *A–C*, nuclear division and degeneration of all but one nucleus in each frustule *D*, enlargement of the protoplasts to form auxospores (*Diagrams based upon Geitler*, 1927*A*)

Auxospores of Centric Diatoms. Auxospores of Centrales are always formed singly within a cell In *Melosira* the halves of a frustule wall pull apart from each other and the exposed portion of the protoplast increases greatly in diameter. It swells to thrice its original size, becomes rounded, and secretes two new silicified half walls with essentially the same markings as the parent cell (Fig 121). This auxospore remains attached to the parent-cell half walls for some time. It germinates by dividing transversely into two daughter cells, and these, in turn, divide and redivide in the same plane. Vegetative daughter cells of an auxo-

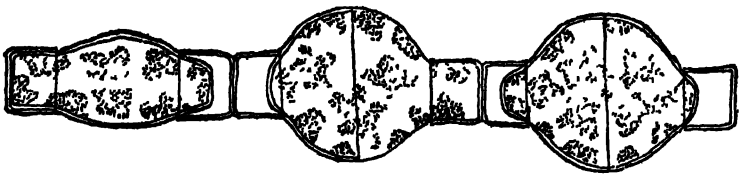


FIG 121.—Auxospores of a centric diatom, *Melosira varians* Ag (*After Pfitzer*, 1882)

[1] Geitler, 1927*A*

spore are the same diameter as the auxospore, that is, two to three times the diameter of the original vegetative cell.

Until a few years ago the auxospores of *Melosira* and of all other Centrales were thought to be strictly asexual. Two species of *Chaetoceros* have recently been described[1] as having a reductional division forming four nuclei. Two of the nuclei fuse, and two generate. One species of *Melosira* has been described as having a similar behavior of the nuclei.[2] Developing auxospores of another species of *Melosira*[3] have been found with one large and two degenerating nuclei. The nuclear behavior in the foregoing cases is not established beyond all doubt, but there is a presumption that auxospore formation is sexual in nature since it involves a fusion of two haploid nuclei. There is also a possibility that auxospores of other Centrales are formed in a similar manner. If this be true, vegetative cells of Centrales are diploid instead of haploid.

"Microspores." Many of the Centrales have been found producing a large number of *microspores* within each cell. The conflicting views concerning the nature of microspores are in part due to the fact that they

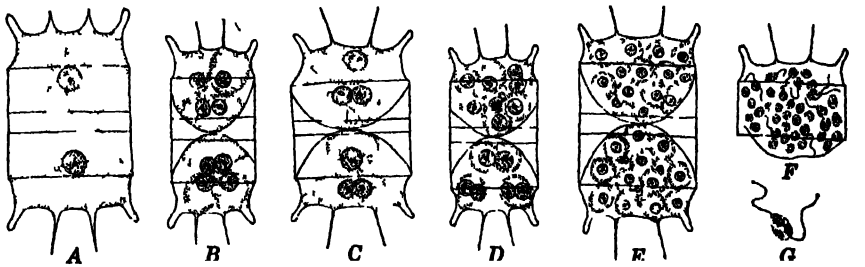


FIG. 122.—Microspore formation in *Biddulphia mobiliensis* Bailey. *A*, recently divided vegetative cell. *B–E* stages in repeated bipartition of protoplasts. *F*, microspores before liberation. *G*, free-swimming microspore. (*After Bergon*, 1907.) (*A–F*, × 200, *G*, × 1,000.)

are known mostly from marine plankton species which have been studied only in preserved collections. However, motile microspores have been demonstrated for a sufficient number of species[4] to warrant the assumption that all have flagella. Microspores of certain genera are described[5] as having one flagellum; those of other species are said[6] to be biflagellate. The number of microspores within a cell is always a multiple of two and there may be 8, 16, 32, 64, or 128 of them. They may be formed by a repeated simultaneous division of the nuclei and a cytoplasmic cleavage

[1] Persidsky, 1929. [2] Persidsky, 1935. [3] Von Cholnoky, 1933*A*.

[4] Bergon, 1907; Pavillard, 1914; Pergallo, 1906; Schiller, 1909; Schmidt, 1923; Went in Geitler, 1932.

[5] Bergon, 1907; Schiller, 1909. [6] Pavillard, 1914; Schmidt, 1923.

following the last series of nuclear divisions,[1] or a cytoplasmic cleavage may follow each nuclear division[2] until 8, 16, 32, or more uninucleate protoplasts have been formed (Fig. 122). All nuclear divisions preceding microspore formation have been held[3] to be equational, but more recent studies[4] indicate that meiosis occurs during the series of divisions.

Some phycologists think that microspores are zoospores; others think that they are zoogametes. The evidence that they are zoogametes is very scanty since gametic union has been found in but one species,[5] and even this is open to question. Even if the fact that microspores are not isogametes can be established beyond all doubt, there is still the possibility that they are gametic in nature. A species of *Chaetoceros* found in a plankton haul from the middle of the Atlantic Ocean and studied in a living condition was found to be liberating motile microspores in abundance.[6] These swarmed about cells with undivided contents. This was thought to be the beginning of a gametic union. If this should prove to be the case, the microspores are to be considered motile male gametes (antherozoids) which escape from a parent cell and swim to a female cell containing an undivided protoplast (the egg).[7] There is also a presumption that the resultant zygote would develop into an auxospore.

Classification. Practically all treatises on diatoms written within the past three decades have followed the classification of Schütt,[8] which is based entirely on structure of the frustule wall. Schutt places all diatoms in a single family and establishes subfamilies, tribes, subtribes, and other family subdivisions to show the affinities between closely related genera and those that are more remotely related. Later workers have raised Schütt's subfamilies to the rank of orders and have given his subdivisions in each subfamily a correspondingly greater rank. Schütt segregated diatoms into two major series, one with ornamentation of valves concentrically or radially symmetrical about a central point, the other with ornamentation of valves bilaterally symmetrical with respect to a line. This distinction appears to be artificial, but it is quite natural and correlates with many other characters. Centric diatoms usually have many chromatophores, are immobile, produce statospores, form motile microspores, and never conjugate in pairs to form an auxospore. Pennate diatoms, on the other hand, usually have but one or two chromatophores, often have cells capable of spontaneous movement, lack flagellated microspores, and frequently conjugate in pairs to form auxospores.

[1] Karsten, 1904; Schmidt, 1929. [2] Bergon, 1907; Hofker, 1928.
[3] Karsten, 1904, 1924. [4] Hofker, 1928; Schmidt, 1931, 1933.
[5] Schmidt, 1923.
[6] Went in Geitler, 1932, pp. 11–12.
[7] Geitler, 1935. [8] Schütt, 1896.

The two orders of diatoms are:

Centrales in which the valves are circular, polygonal, or irregular in outline and with an ornamentation that is radial or concentric about a central point. The valves never have a raphe or pseudoraphe. Living species generally have protoplasts with many chromatophores. There may be a production of statospores or of motile microspores. Auxospores are never formed by a conjugation of two cells. The order includes about 100 genera and 2,400 species.

Pennales in which the valves are bilaterally symmetrical or asymmetrical in surface view, but always with an ornamentation bilaterally disposed with respect to a line and never a point. The valves always have a raphe or pseudoraphe. Living species generally have protoplasts containing one or two chromatophores. There is never a formation of statospores or motile microspores. Cells of many species conjugate in pairs to form auxospores. The order includes about 70 genera and 2,900 species.

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CHAPTER VI

PHAEOPHYTA

Cells of the Phaeophyta, or brown algae, have chromatophores in which the photosynthetic pigments are masked by a golden-brown pigment—*fucoxanthin*. Thalli of Phaeophyta are always multicellular and generally of a definite macroscopic form. Motile reproductive cells, whether zoospores or gametes, are pyriform and have two[1] laterally inserted flagella of unequal length. There are about 190 genera and 900 species of brown algae.[2]

Distribution. Three rare fresh-water Phaeophyta are known from Europe; all other species are marine. Generally speaking, the marine Phaeophyta are algae of cold waters. They are the predominating element in the littoral flora of Arctic and Antarctic seas, and they constitute a progressively less conspicuous element in the flora as one goes toward the tropics. However, certain of the brown algae, notably the Dictyotales and *Sargassum*, are distinctly warm-water plants.

Many of the marine species grow attached to rocks or to some other inanimate substratum. Other species grow in association with other algae, either as epiphytes or as endophytes. In many cases, as *Myrionema strangulans* Grev. (page 248), brown algae grow only upon a single host species.

There is a marked variation in vertical distribution of the marine Phaeophyta at any given station. Many species grow only in the intertidal zone, and even here there is a distinct vertical zonation. Thus the rockweeds (Fucaceae) are usually restricted to the upper littoral belt and the kelps (Laminariales) to the lowermost portion of it. Other littoral genera, as *Sphacelaria* (page 236) and *Leathesia* (page 249), tend to be restricted to the midlittoral belt. There are also species which grow only in the sublittoral region. The most notable of these are certain of the giant kelps found along the Pacific Coast of this country. These algae grow on rocky reefs 10 to 20 meters below the surface of the water. The kelps are anchored to the reef by a holdfast from which arises a long slender axis whose upper portion is expanded into a number of blades that float upon the surface of the water. Other sublittoral

[1] Antherozoids of *Dictyota* appear to have but one laterally inserted flagellum.

[2] Estimates of the number of Phaeophyta are based upon Kjellman, 1891–1893; Kjellman and Svedelius, 1911.

Phaeophyta, as certain species of *Sargassum* (page 224) and of *Desmarestia* (page 253), never extend up to the surface of the water. Sublittoral Phaeophyta of northern seas are rarely found below the 25-meter level, but in warmer waters, as those off the coast of Florida[1] and in the Mediterranean,[2] they may grow at somewhat lower depths. The greatest depth at which brown algae have been found is 110 meters.[2]

Cell Structure. Cells of the Phaeophyta have a distinct wall and one differentiated into an inner firm portion and an outer gelatinous portion. The major constituent of the firm portion is cellulose;[3] that of the gelatinous portion is *algin*, a substance peculiar to brown algae. It is thought[4] that this is a pectic compound which consists in whole[4] or in part[5] of the calcium salt of alginic acid.

Protoplasts of vegetative cells are vacuolate and generally uninucleate. The nuclei resemble those of vascular plants in that there is a nuclear membrane, a nucleolus, and a chromatic network. Their division is mitotic. Division of vegetative nuclei in a considerable number of genera resembles the nuclear division of animals in that there are centrospheres or centrosomes at the polar foci of the mitotic figure. Genera in which these polar bodies have been found include those of Sphacelariales,[6] Cutleriales,[7] Dictyotales,[8] Punctariales,[9] Laminariales,[10] and Fucales.[11] These orders cover such a wide range among the Phaeophyta that one is almost justified in assuming that centrospheres are present in vegetative mitosis in all genera.

Vegetative cells of brown algae generally contain more than one chromatophore. Some species have discoform chromatophores; others have flattened chromatophores with a very irregular outline. The chromatophores lack pyrenoids. The chromatophores or the cytoplasm may contain one or more irregularly shaped whitish *fucosan granules*. At one time the fucosan granules were thought to be an insoluble food reserve stored in the cell. Today[12] they are interpreted as tannic compounds formed as a by-product of metabolic processes within the cell.

Pigments. Chromatophores of brown algae contain the same pigments as the chloroplasts of green plants; that is, chlorophyll *a*, chlorophyll *b*, carotin, and xanthophyll. Pigments in the brown algae are thought[13] to be similar in chemical composition to those in the green plant.

[1] Taylor, 1928. [2] Funk, 1927.
[3] Kylin, 1915; Miwa, 1932; Naylor and Russell-Wells, 1934.
[4] Kylin, 1915. [5] Miwa, 1932.
[6] Higgins, 1931; Swingle, 1897. [7] Yamanouchi, 1912, 1913.
[8] Carter, 1927; Haupt, 1932; Mottier, 1900; Williams, 1904, 1904*A*.
[9] Mathias, 1935. [10] McKay, 1933.
[11] Farmer and Williams, 1898; Strasburger, 1897; Walker, 1931; Yamanouchi, 1909.
[12] Chadefaud, 1936; Kylin, 1912, 1918.
[13] Kylin, 1912*A*, 1927; Willstätter and Page, 1914

However, the proportional amounts of chlorophyll *a* and chlorophyll *b* are different[1] since chromatophores of brown algae contain less than 5 per cent chlorophyll *b*. The unique pigment of the Phaeophyta, fucoxanthin, masks the other pigments in the chromatophore. It is a carotinoid pigment, and its chemical composition has been given[1] as $C_{40}H_{54}O_6$. More recently it has been held[2] that the so-called fucoxanthin is really a mixture of two carotinoid pigments, fucoxanthin *a* and fucoxanthin *b*.

Reserve Foods. Carbohydrate formation in brown algae is comparable to that in sugar-storing vascular plants rather than to that in starch-storing ones. All reserve carbohydrates of Phaeophyta are stored in a dissolved state; but it is uncertain whether these accumulate in the vacuoles, in the cytoplasm, or throughout the protoplast. Cells of brown algae contain only very small amounts of simple sugars[3]—probably pentoses.[4] It is not improbable that the simple sugars formed by photosynthesis are immediately converted into more complex carbohydrates. One of the most widely distributed of these[5] is a dextrin-like polysaccharide known as *laminarin*. It has been held[6] that the so-called laminarin is really a series of closely related compounds rather than a single one. Laminarin may accumulate in sufficient quantity to constitute 7 to 35 per cent of the dry weight of a plant.[6] The gradual increase in the amount of laminarin throughout the growing season and the diminution in the amount of it at the time of reproduction or when new parts are regenerated shows that it serves as a reserve food.[6] Another widely distributed carbohydrate of Phaeophyta is *mannitol*, a hexahydric alcohol.[7] Some of the brown algae also form a certain amount of fats or fat-like substances. These are especially abundant in species growing high in the littoral zone.[8]

The Thallus. In all of the Phaeophyta but the Fucales there is, or there probably is, an alternation of a free-living multicellular gametophytic generation with a free-living multicellular sporophytic generation. The two generations may be similar in size and vegetative structure, or they may be dissimilar. Genera with dissimilar generations may have the sporophyte larger than the gametophyte, or vice versa. In some genera, as *Leathesia* (page 249), both generations are annual plants; in other genera, as *Zonaria* (page 244), both are perennial; in still others, as in certain kelps, the gametophyte is an annual and the sporophyte a perennial.

[1] Willstatter and Page, 1914. [2] Kylin, 1927.
[3] Haas and Hill, 1933; Kylin, 1918*A*. [4] Haas and Hill, 1929.
[5] Kylin, 1913, 1915, 1918*A*. [6] Kylin, 1915.
[7] Haas and Hill, 1929*A*; Kylin, 1913, 1918*A*. [8] Haas and Hill, 1933.

There is great variation in size of the adult thallus from genus to genus. At one extreme stand the minute gametophytes or sporophytes with only a few cells; at the other extreme are the sporophytes of the Pacific Coast giant kelps that attain a height of 25 to 30 meters. There is no particular correlation between longevity and size of the plant body. Thus, among the sporophytes of kelps, that of *Nereocystis* is an annual which grows to a height of 15 to 20 meters, whereas that of *Pterygophora* lives for 15 years or more and never becomes more than 3 meters tall.

The mature sporophyte or gametophyte may either be amorphous or of definite form. In the latter case it is generally differentiated into a holdfast and an erect portion. The erect portion may be simple or branched; solid or hollow; and tubular, spherical, or compressed. The greatest complexity of form is found among the kelps where there is an external differentiation comparable to that of a vascular plant. There is a root-like holdfast from which arises a simple or branched stem-like stipe that bears one to many leaf-like blades.

The growing apex of many Phaeophyta is a branched uniseriate filament in which cell division is intercalary. Growth by means of such an apical filament is said to be *trichothallic*. In some trichothallic genera mature portions of a thallus have a filamentous organization similar to that of the growing apex This is clearly evident in genera where the branches lie free from one another, as in *Ectocarpus* (page 232), and it is less clearly evident in genera, such as *Leathesia* (page 249), where the branches lie apposed to one another. In still other genera, as *Desmarestia* (page 253), the trichothallic nature of mature portions of a thallus is completely obliterated by a cortication of the filaments.

Terminal growth of other Phaeophyta is initiated by a single apical cell (*Pelvetia*, page 268), or a transverse row of apical cells (*Zonaria*, page 244). According to the species, the apical cell cuts off derivatives at the posterior face only, or at both the posterior and the lateral faces.

Growth of the kelps is unique in that it is not apical, but is due to the activity of a meristematic region at the juncture of stipe and blade, or at the base of the stipe.

Mature regions of most thalli have more or less differentiation between the external and the internal portions. Superficial cells are always smaller and more densely filled with chromatophores than are the internal ones. The transition from small superficial to large internal cells may be gradual (*Leathesia*, page 249), or the superficial cells may be differentiated into an epidermis-like layer (*Desmarestia*, page 253). Thalli of Fucales and Laminariales are internally differentiated into two distinct tissues; the central *medulla*, composed of elongate colorless cells, and the encircling *cortex* of more or less isodiametric cells in which

those toward the exterior contain chromatophores. The greatest internal differentiation of tissues is found in certain Pacific Coast giant kelps where there are sieve tubes among the elements of the medulla.

Asexual Reproduction. Several of the Phaeophyta reproduce vegetatively by a fragmentation of the thallus. This may take place at either the juvenile or the adult stage. An attached adult thallus may split into two or more portions which remain attached to the substratum. In such cases a single individual may be replaced by a cluster of individuals. Vegetative multiplication may also be effected by a detachment of fragments that float away and develop into new plants. The best example of multiplication by means of detached fragments is the *Sargassum*, which is abundant in the Gulf Stream and the Sargasso Sea. The most prolific of these *Sargassa* is *S. natans* (L.) Meyen, a species known only in the free-floating condition and one which has never been found with fructifications.[1] Vegetative multiplication may also be due, as in *Sphacelaria* (page 236), to the formation and abscission of special reproductive branches, *propagula*.

All Phaeophyta but the Fucales produce either zoospores or aplanospores. Zoospores may be formed within one-celled or within many-celled reproductive organs. The widespread usage of the name that Thuret[2] gave the many-celled organ (*plurilocular sporangium*) is misleading since it is applied both to many-celled sporangia and to many-celled gametangia.

The one-celled zooid-producing reproductive organ that Thuret called a *unilocular sporangium* is sporangial in nature. Its development begins with an enlargement of a uninucleate cell and a division and redivision of the nucleus into 32, 64, or 128 daughter nuclei. There is then a cleavage into uninucleate protoplasts, not separated from one another by walls, and a metamorphosis of each protoplast into a biflagellate zoospore. The zoospores are liberated by a rupture of the sporangial wall. In all species that have been investigated cytologically,[3] the thallus producing unilocular sporangia is diploid, and the first nuclear division in sporangial development is reductional. Hence one is justified in assuming that any thallus producing unilocular sporangia is diploid and not haploid. Thalli have been grown in cultures initiated by inoculation with zoospores from unilocular sporangia of 50 or more species and in every case these have been gametophytes. Some phycologists[4] hold that the zoospores from unilocular sporangia always germinate to form

[1] Collins, 1917. [2] Thuret, 1855.

[3] Clint, 1927; Dammann, 1930; Higgins, 1931; Knight, 1923, 1929; Kylin, 1918*B*; McKay, 1933; Mathias, 1935, 1935*A*; Parke, 1933; Pappenfus, 1935; Yamanouchi, 1912, 1913.

[4] Kylin, 1933.

gametophytes, but in several genera the zoospores have been observed[1] fusing in pairs. Unfortunately, practically nothing is known concerning further behavior of these zygotes.

Unilocular sporangia may also have their protoplasts dividing into large nonflagellated aplanospores instead of into zoospores. In the Dictyotales the single nucleus of a young sporangium divides reductionally[2] to form four or eight nuclei. This is followed by a cleavage of the protoplast into four or eight uninucleate aplanospores. The *monosporangium* of the Tilopteridales also seems to be a unilocular sporangium (see page 238).

The nature of the so-called *plurilocular sporangium* was a matter of dispute until the introduction of the culture method of studying life histories some twenty years ago. This has shown that some "plurilocular sporangia" are gametangia, and others are sporangia. When a plurilocular sporangium is a sporangium, it is always borne upon a diploid thallus, and the zoospores produced by it germinate to form new diploid plants. These have been called[3] *neutral zoospores*, because they germinate to form the same instead of the alternate generation. The sporangium producing them should be called a *neutral sporangium* rather than a plurilocular sporangium. The neutral sporangium develops from a single cell which divides and redivides to form an elongate multicellular structure composed of many small cubical cells (Fig 125*J-I*). Neutral sporangia of most Phaeophyta are many cells in height and several in breadth, but in some genera (as *Leathesia*, Fig. 138*B*) they are one cell in breadth and a few cells in height. The protoplast of each cell in a sporangium is eventually metamorphosed into a neutral zoospore with two laterally inserted flagella. Neutral zoospores are liberated by a rupture of the surrounding cell walls. A few of the brown algae are heterosporous and with two morphologically different neutral sporangia, one producing small zoospores, the other large ones.[4]

Sexual Reproduction. Gametic union among Phaeophyta may be by a union of two motile gametes of equal size (*isogamy*), by a union of two motile gametes of unequal size (*anisogamy*), or by a union of a small motile antherozoid with a large immobile egg (*oogamy*). Gametangia producing iso- and anisogametes have a structure similar to that of neutral sporangia. Sexual reproduction in most of the Ectocarpales, Sphacelariales, Punctariales, and Dictyosiphonales is isogamous. The gametophytes may be homo- or heterothallic. Both isogametes may be actively motile at the time of gametic union, or one of them (the female)

[1] Abe, 1935, 1935*A*; Cl[illegible]t, 1927; Hygen, 1934; Knight, 1929; Schussnig and Kothbauer, 1934.

[2] Carter, 1927; Haupt, 1932; Mottier, 1900; Williams, 1904.

[3] Svedelius, 1928 [4] Sauvageau, 1896; Svedelius, 1928.

may be motionless at the time when the other (the male) swims to and unites with it. Gametic union is immediately followed by a development of the zygote into a sporophyte. There is usually a disintegration of gametes that have failed to conjugate, but sometimes[1] they develop parthenogenetically into new gametophytes.

Relatively few of the brown algae are anisogamous.[2] Gametangia of anisogamous species are multicellular and morphologically different. Male gametangia are distinguishable from female ones on account of their much smaller cells. Both kinds of gamete are biflagellate. Male gametes usually have but one chromatophore, and the female gametes usually contain several. At the time of gametic union the male gametes are actively motile, and the female immobile or moving sluggishly. In the Cutleriales[3] fusion of the two nuclei takes place within a few hours after gametic union, and the zygote begins to develop into a sporophyte within a day. Unfertilized female gametes of Cutleriales regularly develop parthenogenetically into new gametophytes.[3]

Thus far, all known gametophytes of Desmarestiales, Laminariales, and Dictyotales are oogamous and heterothallic. The antheridia may be multicellular (Dictyotales) or unicellular (Desmarestiales, Laminariales). These two types of antheridium are homologous with gametangia producing iso- or anisogametes in that the entire protoplast within an antheridial cell is metamorphosed into a single biflagellate antherozoid. The oögonia are always unicellular and with a single large nonflagellated egg. Eggs of the Dictyotales are discharged from the oogonia, and fertilization takes place while they are floating about in the water. Those of Desmarestiales and Laminariales are extruded from, but remain attached to, the apices of the oogonia. Parthenogenesis is quite common in the Dictyotales, an order in which sporophyte and gametophyte are identical. It has also been found in two oogamous species of a genus in which gametophyte and sporophyte are dissimilar. Here[4] the parthenogenetically developed germling has the structure of a sporophyte.

All the Fucales are oogamous. Depending upon the genus, one, two, four, or eight "eggs" are formed with a one-celled reproductive organ which is usually called an "oogonium." The "antherozoids," generally 64, are formed within a one-celled reproductive organ which is usually called an "antheridium." Antherozoids of Fucales differ from those of all other brown algae in that the posterior flagellum is longer than the anterior one. Oogonia and antheridia of Fucales differ from those of all other oogamous Phaeophyta in that they are borne upon a diploid plant. Young "sex organs" of Fucales contain a single diploid nucleus which

[1] Hygen, 1934; Pappenfuss, 1935
[2] Kuckuck, 1912A; Sauvageau, 1896A; Yamanouchi, 1912, 1913
[3] Yamanouchi, 1912, 1913 [4] Schreiber, 1930.

divides reductionally as the organ develops. Thus, as first pointed out by Kylin,[1] reproductive organs of Fucales are homologous with unilocular sporangia rather than with gametangia. All the Fucales are heterosporous and with *microsporangia*[2] that produce small motile spores and *macrosporangia*[2] that produce large immobile ones. All the Fucales regularly have a gametic union in which the microspores (zoospores) function as antherozoids and the macrospores (aplanospores) function as eggs. Under normal conditions unfertilized eggs disintegrate a few hours after liberation, but they have been induced[3] to germinate parthenogenetically by chemical stimulation.

Alternation of Generations. The epoch-making discovery[4] of an alternation of generations in the Laminariales was due to an introduction

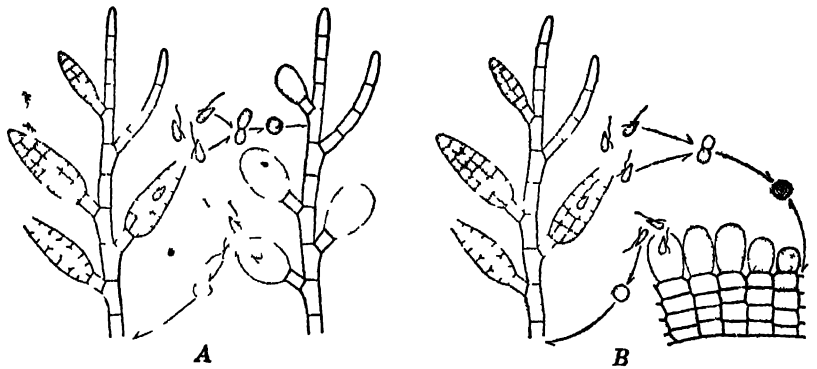


FIG. 123.—Diagrams showing the typical life cycle of a member of the Isogeneratae (*A*) and a member of the Heterogeneratae (*B*). Cells containing diploid nuclei are outlined with a heavy line.

of culture methods in investigating life cycles. The results obtained by cultivation of a wide range of Phaeophyta now justify the generalization[5] that all brown algae but the Fucales have an alternation of sporophyte and gametophyte.

Gametophyte and sporophyte may be alike in vegetative structure, or the two may be markedly unlike (Fig. 123). Usually one cannot be certain concerning the similarity or dissimilarity of the two generations until a genus has been studied in controlled culture. If any plant brought into the laboratory bears unilocular sporangia, one may be certain that it is a sporophyte. The same cannot be said for any brown alga bearing only "plurilocular sporangia," since these may be gametangia borne upon a gametophyte or neutral sporangia borne upon a sporophyte.

Some Phaeophyta have a life cycle in which there is an obligatory alternation of gametophyte and sporophyte. Both generations may be

[1] Kylin, 1917. [2] Taylor, 1928. [3] Overton, 1913.
[4] Sauvageau, 1915. [5] Kylin, 1933.

annual plants, both may be perennial, or one may be annual and the other perennial. Many Phaeophyta have the regular alternation of sporophyte and gametophyte complicated by a reduplication of the sporophyte by means of neutral spores. Production of neutral sporangia is generally accompanied by a reduction in the number of unilocular sporangia. Sometimes there is a complete suppression of unilocular sporangia. Reduplication of the sporophyte by means of neutral spores may be seasonal, as in *Ectocarpus siliculosus* Dillw. (page 233), or it may continue throughout the year. The life cycle in these genera producing only[1] neutral spores is merely a succession of sporophytic generations.

The life cycle may be further complicated by reproduction at a state when the thallus is a small plantlet. In certain cases the plantlets are evidently juvenile and either a gametophytic *protonema*[2] or a sporophytic *diplonema*.[3] Reproduction of protonemata and diplonemata is always vegetative. Other Phaeophyta produce dwarf stages (*plethysmothalli*)[2] with reproductive organs, either unilocular or neutral sporangia. Plethysmothalli of most, if not all, brown algae are developed during the winter. There are certain structural differences between the plethysmothallus and the juvenile stage (diplonema) of an adult sporophyte. These are not wholly due to growth responses to a decrease in temperature and illumination because, as in *Leathesia*,[4] chromatophores in cells of diplonemata and plethysmothalli may differ in number and in structure. Germinating neutral spores from a plethysmothallus may develop into a typical sporophyte or into another plethysmothallus.[5] Thus the plethysmothallus is really an intercalated third type of generation in the life cycle.

Many Phaeophyta with alternating sporophytes and gametophytes have one or more of the accessory methods of reproduction mentioned above. The gametophyte may be reduplicated either by vegetative multiplication or by a parthenogenetic germination of gametes. The zygote may develop into a plethysmothallus or into a typical sporophyte. A plethysmothallus may produce either neutral spores or zoospores; the former germinating to form either plethysmothalli or typical sporophytes, the latter germinating to form gametophytes. Sporophytes may be reduplicated by neutral spores, by gametic union of zoospores, or by vegetative multiplication at diplonematal or at adult stages. All of the foregoing are theoretically possible in the life cycle of a single species, but as yet no such species is known.

The Fucales have a life cycle in which there is an alternation of a sporophytic generation with a one-celled haploid phase. Many phycol-

[1] Kylin, 1933. [2] Sauvageau, 1928. [3] Hygen, 1934.
[4] Sauvageau, 1932. [5] Sauvageau, 1932, 1933.

ogists accept the hypothesis[1] that the nuclear generations subsequent to meiosis in micro- and macrosporangia are the equivalent of a gametophytic generation. However, this overlooks the fact that Phaeophyta with a true gametophytic generation have similar nuclear generations following meiosis in their unilocular sporangia.

Origin and Evolution of Phaeophyta. The fundamental metabolic features of brown algae are so distinctive that they do not appear to be related to, or derived from, other algae. It is very probable that the Phaeophyta are a series of considerable antiquity, but undoubted fossil members of the division have not been found earlier than the Triassic.[2]

The universal presence of motile reproductive cells among Phaeophyta indicates that they arose from a unicellular flagellated ancestor. Certain

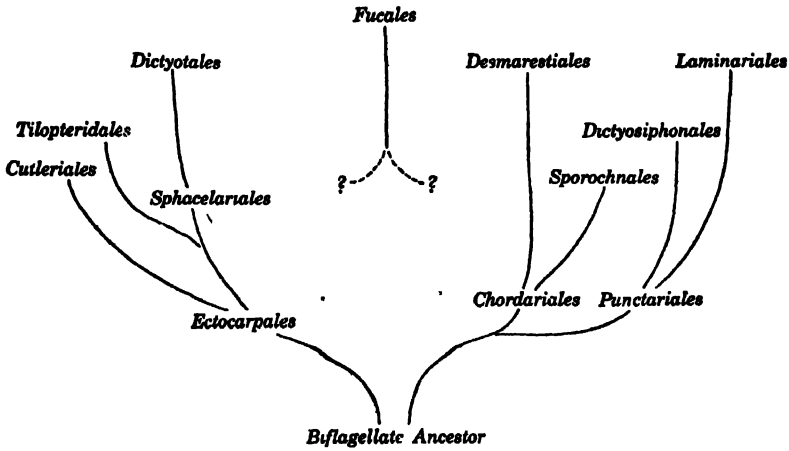


FIG. 124.—Diagram showing the suggested interrelationships among the Phaeophyta.

of the present-day fresh-water flagellated organisms with brown chromatophores were at one time thought to be analogous to ancestors of the brown algae, but all of them are now placed in another algal series—the Chrysophyta. All of the present-day Phaeophyta are multicellular, and there are no known connecting links with the hypothetical unicellular flagellated ancestors. One explanation for this absence of primitive brown algae is that they were evolved in the ocean at a time when it was much less saline than at present, and that there was a dying off of the more primitive forms as the salinity of the ocean increased. However, this plausible suggestion fails to explain why there was not a migration of them from the fresh-water ocean to inland fresh waters of the early land masses.

There is good reason for believing that two divergent series were established early in evolution of the Phaeophyta; one with an alternation

[1] Strasburger, 1906. [2] Pia, 1927.

of similar gametophytes and sporophytes, the other with an alternation of dissimilar generations (Fig. 124). In both series there was a progressive evolution from isogamy to oogamy, and in both of them the thallus structure became increasingly complex.

The relationships of the Fucales to other brown algae are obscure. It has been held[1] that they are a series independent from those Phaeophyta with an alternating sporophyte and gametophyte. If the Fucales are an independently evolved series, one would expect that there would also be simpler Phaeophyta with a fucaceous type of life cycle. Since there are no such forms, it seems more probable that the Fucales arose by a dropping out of the gametophyte generation in a complex heterosporous brown alga with two alternating generations. There is nothing to indicate whether this hypothetical ancestor had similar or dissimilar alternating generations.

Classification. Before 1922 all systems for classification of Phaeophyta were based upon structure and the method of reproduction. That year one was proposed[2] which took life cycles into account, but the data for an adequate classification were then insufficient. Sufficient data have now accumulated to classify the major series of Phaeophyta solely on the basis of the life cycle.[3] According to such a basis the Phaeophyta fall into the following three classes:

Isogeneratae in which there is an alternation of two similar generations

Heterogeneratae in which there is an alternation of two dissimilar generations.

Cyclosporeae in which there is only a diploid generation.

CLASS 1. ISOGENERATAE

The Isogeneratae have a life cycle with two alternating generations that are identical in vegetative structure. Growth of the thallus may be trichothallic, intercalary, or strictly apical. Thalli may be amorphous or of definite form and with or without an internal differentiation. The sporophytic generation may produce zoospores, aplanospores, or neutral spores. Sexual reproduction of the gametophyte may be isogamous, anisogamous, or oogamous.

The class is divided into five orders differing from one another in vegetative structure, method of growth, and structure of reproductive cells.

ORDER 1. ECTOCARPALES

The Ectocarpales have a branched filamentous thallus in which growth is trichothallic. Reproductive organs may be borne singly or in a uni-

[1] Kylin, 1933. [2] Taylor, 1922. [3] Kylin, 1933; Taylor, 1936.

seriate row. Those of the sporophyte produce either zoospores or neutral spores, and those of the gametophyte produce isogametes.

Systems of classification based wholly upon structure and method of reproduction refer many genera to the Ectocarpales. When, as here, the order is restricted to trichothallic filamentous Phaeophyta with a known or suspected alternation of similar generations, it does not include more than four or five genera, all placed in a single family—the Ectocarpaceae.

The type genus, *Ectocarpus*, is world wide in distribution and contains many species. The genus is a common one along the Atlantic Coast of this country, and certain species grow in abundance upon Fucaceae of the upper littoral zone. It is a scarcer genus along the Pacific Coast, where most of the species grow upon Laminariales.

The thallus is sparingly to profusely branched, with the cells joined end to end in a single series (Fig. 125*A*). It is differentiated into a prostrate attached portion and an erect portion. The prostrate portion is irregularly and more or less profusely branched; the erect portion is a branched tuft in which the ultimate branchlets are generally attenuated to an acute point. In some species the older portions of major branches are ensheathed (corticated) by a layer of descending rhizoidal branches. Cells of *Ectocarpus* are uninucleate and either with a few band-shaped chromatophores of irregular outline or with many small disk-shaped chromatophores.

Reproduction is by means of biflagellate zooids produced within unilocular reproductive organs or within plurilocular ones. These are usually borne terminally and singly on lateral branchlets, but in rare cases they are borne seriately.

Development of a unilocular sporangium begins with an enlargement of the terminal cell of a short lateral branchlet The young sporangium becomes ellipsoidal and enlarges to several times its original size, with a considerable increase in the number of chromatophores. The single nucleus within a young sporangium divides, its daughter nuclei divide, and simultaneous division of their daughter nuclei continues until there are 32 or 64 nuclei. Division of the original nucleus is reductional and that of the daughter nuclei is equational. When nuclear division ceases, there is a cleavage into uninucleate protoplasts, each with a single chromatophore. Each protoplast is then metamorphosed into a pyriform zoospore, in which the longer of the two laterally inserted flagella is directed forward and the shorter is directed backward. The zoospores are extruded en masse through a small opening at the distal end of the sporangial wall. Individual zoospores of the extruded mass remain quiescent for from 30 to 60 seconds: then they become motile and swim freely in all directions. After zoospores have been discharged from a

sporangium, there may be a proliferation of a new sporangium within the old sporangial wall.

Plurilocular reproductive organs, whether gametangia or neutral sporangia, also develop from the terminal cell of a lateral branchlet. Repeated transverse division of this cell produces a vertical row of 6 to 12 cells (Fig. 125*D–F*). Beginning with median members of the row,

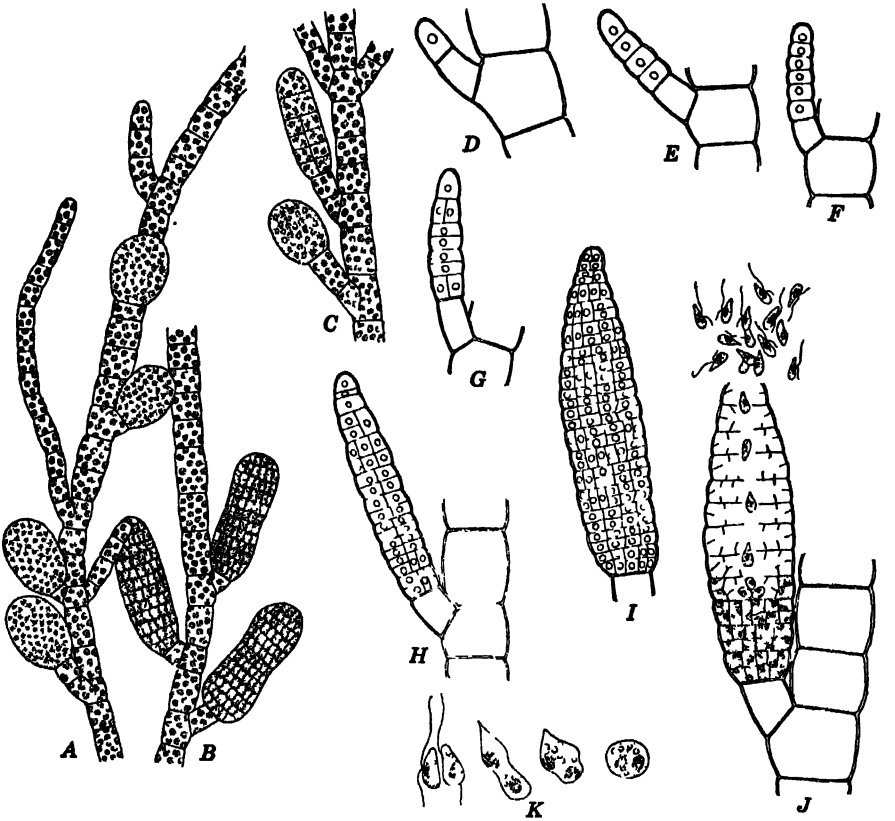


FIG. 125.—*Ectocarpus cylindricus* Saunders. *A*, thallus with unilocular sporangia. *B*, portion of thallus with neutral sporangia. *C*, portion of a thallus bearing both unilocular and neutral sporangia. *D–J*, *E. acutus* Setchell and Gardner. *D I*, stages in development of neutral sporangia. *J*, liberation of neutral spores *K*, *E siliculosus* (Dillw.) Lyngb. gametic union. (*K After Kuckuck*, 1912*A*). (*A–C*, × 120; *D–J*, × 650; *K*, × 600.)

there is then a vertical division of all cells (Fig. 125*G–H*). Repeated vertical and transverse division continues until there are several hundred small cubical cells arranged in 20 to 40 transverse tiers (Fig. 125*I*). The protoplast of each cell is then metamorphosed into a single biflagellate zooid. Liberation of the zooids is gradual and is through a terminal or a lateral pore. Zooids just beneath the pore escape in an irregular mass; those more remote from it move out in a single file and in an orderly procession (Fig. 125*J*).

Reproduction has been most thoroughly investigated in *E. siliculosus* Dillw. The nature of zooids from plurilocular organs of this species was long a matter of dispute among European phycologists, since those studying plants from Mediterranean waters repeatedly found gametic union and those studying plants from North European waters never found it. These discrepancies have been reconciled within the past decade by studies following development from zooid to mature fruiting plant in controlled culture and by studies on the nuclear cycle. All cytological investigations of the species[1] show that diploid plants with unilocular and plurilocular sporangia have a reduction division in the

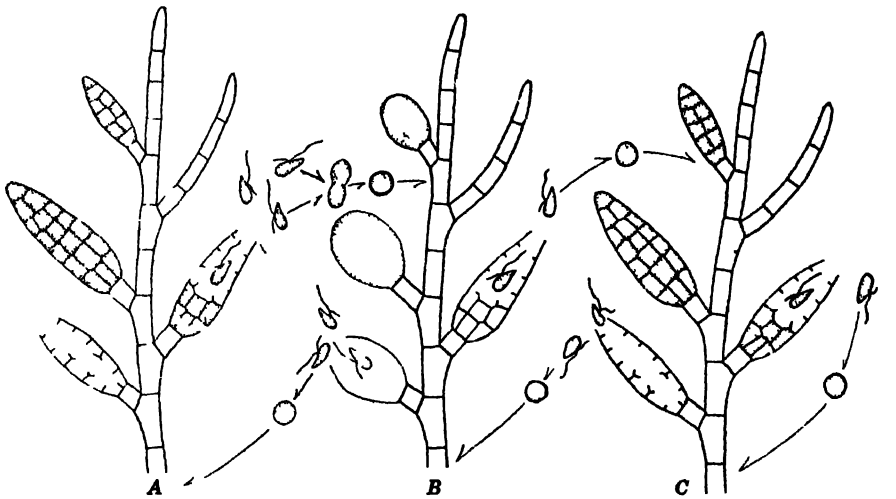


FIG. 126.—Diagram showing variations in the life cycle of *Ectocarpus*. Cells containing diploid nuclei are outlined with a heavy line.

former and none in the latter. Diploid zooids from neutral (plurilocular) sporangia germinate to form sporophytes which bear either unilocular or neutral sporangia.[2] Zoospores from unilocular sporangia develop into gametophytes whose gametes may either unite in pairs or develop parthenogenetically into new gametophytes.[3] Germination of a zygote produces a new sporophyte. A gametic pairing of zoospores from unilocular sporangia has also been recorded,[4] but nothing is known concerning further development of this fusion product. Thus, in addition to a regular alternation of generations, *E. siliculosus* may have a reduplication of either generation (Fig. 126). Reduplication of the sporophyte is by means of neutral spores and possibly by a gametic union

[1] Knight, 1929; Pappenfuss, 1935; Schussnig and Kothbauer, 1934.
[2] Knight, 1929; Kylin, 1933; Pappenfuss, 1935. [3] Pappenfuss, 1935.
[4] Knight, 1929; Schussnig and Kothbauer, 1934.

of zoospores; that of the gametophyte is by a parthenogenetic germination of gametes.

Environmental conditions, possibly temperature or duration and intensity of illumination, have a direct effect on the life cycle of *E. siliculosus*. Plants growing in Swedish[1] and British[2] waters are exclusively sporophytic, and there does not seem to be a development of the alternate gametophyte even when unilocular sporangia produce haploid zoospores in abundance. In Mediterranean waters near Naples the plants have been reported[2] as exclusively gametophytic, but sporophytes have been found[3] in this region. There seems to be a regular formation of zygotes from gametes of the Naples plants but only an occasional development of sporophytes from the zygotes. In this country, both gametophytes and sporophytes have been found in abundance at Woods Hole, Massachu-

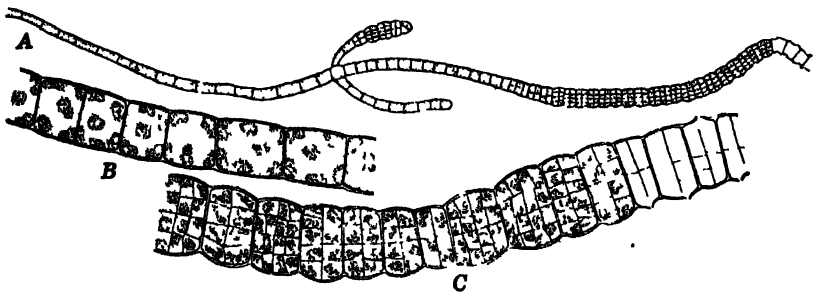


FIG. 127.—*Pylaiella Gardneri* Collins. *A*, upper portion of a thallus *B*, vegetative cells *C*, neutral sporangia before and after liberation of spores (*A*, × 120, *B* (, × 485)

setts.[4] The sporophytes grow throughout the year and upon several hosts. Neutral sporangia are present at all seasons, and unilocular sporangia during the summer months only. The gametophytes grow upon a single host (*Chordaria*) and have been found in fruit from midsummer to early fall. However, the available data are too fragmentary to justify any conclusions concerning the length of the gametophyte's fruiting period. Both the Woods Hole and the Naples plants are heterothallic.

Pylaiella is the only other thoroughly investigated genus of the Ectocarpales. The commonest species along the Atlantic Coast is *P. littoralis* (L.) Kjellm., which is epiphytic on various Fucaceae; that along the Pacific Coast is *P. Gardneri* Collins (Fig. 127), epiphytic upon the sea palm (*Postelsia*). The thallus of *Pylaiella* is differentiated into a prostrate and an erect portion, but the latter may be very sparingly branched. The genus differs from *Ectocarpus* in that reproductive organs, both uni- and plurilocular, are borne in intercalary series.

[1] Kylin, 1933 [2] Knight, 1929.
[3] Schussnig and Kothbauer, 1934. [4] Pappenfuss, 1935.

P. littoralis has an alternation of generations and one in which the number of chromosomes is halved[1] when zoospores are formed within the unilocular sporangia. In England[2] the two generations usually grow upon different Fucaceae; the gametophyte upon *Ascophyllum* and the sporophyte upon *Fucus*. In addition to an alternation of generations, *P. littoralis* may have the sporophyte reduplicated by neutral spores.

The sporophytes seem to be perennials which produce unilocular sporangia throughout the year.[3] The gametophytes seem to be annuals, which develop to maturity, fruit, and die during the spring and summer. This indicates that there is but little germination of haploid zoospores liberated during autumn and winter.

ORDER 2. SPHACELARIALES

Growth of thalli of Sphacelariales is initialed by a single large apical cell. The two generations are alike in vegetative structure and have their cells regularly arranged in transverse tiers. The sporophyte may produce haploid zoospores or diploid neutral spores; gametes produced by the gametophyte may be isogamous or anisogamous.

The order includes some 10 genera and 60 species. These are divided into three families. The order is a natural one whose members are easily distinguishable from other Phaeophyta on account of their polysiphonous organization, in which the cells are vertically elongated and regularly arranged in transverse tiers.

The type genus, *Sphacelaria*, is a rather rare alga along both the Atlantic and Pacific coasts of this country. It grows attached to rocks or to other algae by means of a small, more or less disk-shaped holdfast. One or more freely branched shoots arise from the holdfast. Each branch terminates in a conspicuous, uninucleate, cylindrical, apical cell (Fig. 128*A*). Division of the apical cell is always transverse. Derivatives two to four cells posterior to an apical cell divide and redivide in a vertical plane to form a transverse tier of 4 to 20 vertically elongate cells. Branching of a shoot is due to an enlargement of a cell in the polysiphonous portion and to its functioning as an apical cell. Some species have multicellular hairs in which the cells are arranged in a single row (Fig. 128*B*). Initials developing into hairs are formed by an asymmetrical diagonal division of the apical cell.[4] Vegetative cells of *Sphacelaria* contain a single large nucleus and many small discoform chromatophores.

Many species reproduce vegetatively by means of *propagula*,[5] and at certain seasons of the year they are the only means of multiplication. Development of a propagulum (Fig. 128*D–G*) begins in the same manner as that of a lateral branch, but, after it has become a few cells long,

[1] Damman, 1930; Knight, 1923. [2] Knight, 1923.
[3] Kylin, 1933. [4] Sauvageau, 1900–1901.

there is a vertical division of the apical cell into two or three daughter cells. Each daughter cell is the initial of a branch. The bi- or triradiate branch system at the apex of a propagulum may remain short and massive, or become long and slender. Eventually there is an abscission

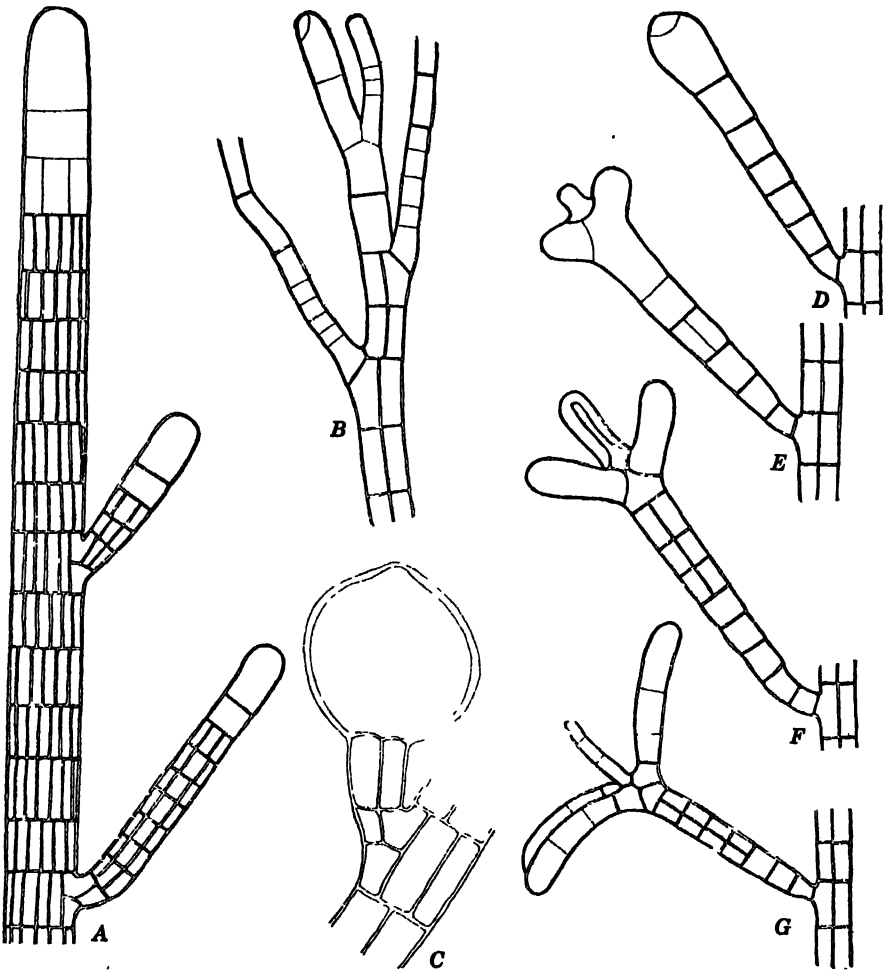


FIG. 128.—*A*, apex of thallus of *Sphacelaria californica* Sauv. *B-G*, *S. radicans* (Dillw.) Harv. *B*, hairs. *C*, unilocular sporangium. *D-G*, stages in development of propagula. (*A*, *D-G*, × 160; *B*, × 215; *C*, × 325.)

of the propagulum at the point where it is attached to the thallus. It floats away, lodges upon a favorable substratum, and there develops into a new thallus.

Zooids may be produced within unilocular or plurilocular reproductive organs. *Sphacelaria*[1] and certain other genera[2] of the order are known

[1] Clint, 1927. [2] Higgins, 1931; Knight, 1929; Mathias, 1935*A*.

to have a reduction division of the nucleus within a young unilocular sporangium (Fig. 128*C*). Mature unilocular sporangia of *S. bipinnatus* Sauv. contain more than 200 zoospores,[1] presumably 256. They are discharged through an apical pore in the sporangial wall from which they swim away individually soon after liberation. Germlings from zoospores have been grown in culture,[2] but none of them have developed into mature gametophytes. Sporophytes with unilocular sporangia may also bear neutral sporangia.[3] From what is known concerning the neutral spores of other Phaeophyta, there is no doubt but that those of *Sphacelaria* are diploid and develop directly into new sporophytes.

The gametophytes produce many-celled gametangia. Some species are isogamous, others are anisogamous[4] and have male gametangia distinguishable from female ones on account of their smaller cells. Gametangia may be solid,[1] as in *Ectocarpus*, or they may be elongate, hollow, multicellular sacs, one cell in thickness.[4] Liberation of gametes differs from that of *Ectocarpus* in that a pore is formed by each cell of the gametangium, and there is a simultaneous instead of a gradual liberation of the gametes.[1] Gametic union of the isogamous *S. bipinnata* takes place while both gametes are actively motile and produces a quadriflagellate zygote that may continue swarming for several hours.[1] Although not confirmed by growth in controlled culture, there is little doubt but that *Sphacelaria* and other members of the order have an alternation of generations and a life cycle in which the sporophyte may be reduplicated by neutral spores.

ORDER 3. TILOPTERIDALES

Thalli of Tilopteridales are freely branched and with a trichothallic mode of growth. Upper portions of them are *Ectocarpus*-like with the cells joined end to end in a single row (*monosiphonous*); lower portions are generally *Sphacelaria*-like with the cells in transverse tiers (*polysiphonous*). The available evidence, although incomplete, indicates that there is an alternation of similar generations. The sporophyte produces unilocular sporangia, each containing a single quadrinucleate aplanospore. The gametophyte seems to be oogamous.

The order includes about 5 genera and 10 species.

Haplospora, with the single species *H. globosa* Kjellm., is known from England and the Scandinavian Peninsula. It has a freely and alternately branched thallus[5] in which the upper portion is monosiphonous and the lower portion polysiphonous (Fig. 129). Cells of both the mono- and

[1] Pappenfuss, 1934. [2] Clint, 1927; Pappenfuss, 1934.
[3] Pappenfuss, 1934; Sauvageau, 1900–1904. [4] Sauvageau, 1900–1904.
[5] Brebner, 1896; Reinke, 1889.

polysiphonous portions contain many small discoform chromatophores. The thallus is attached to the substratum by means of rhizoids.

Reproduction is by means of large quadrinucleate aplanospores (*monospores*) formed singly within globose sporangia borne terminally on short lateral branchlets. The demonstration[1] of a reduction division when the four nuclei are formed within a sporangium shows that the plant bearing sporangia is a sporophyte. Sporangia of *H. globosa* are homologous with unilocular sporangia of other Phaeophyta, but they are of a unique type in that there is not a cleavage of the quadrinucleate

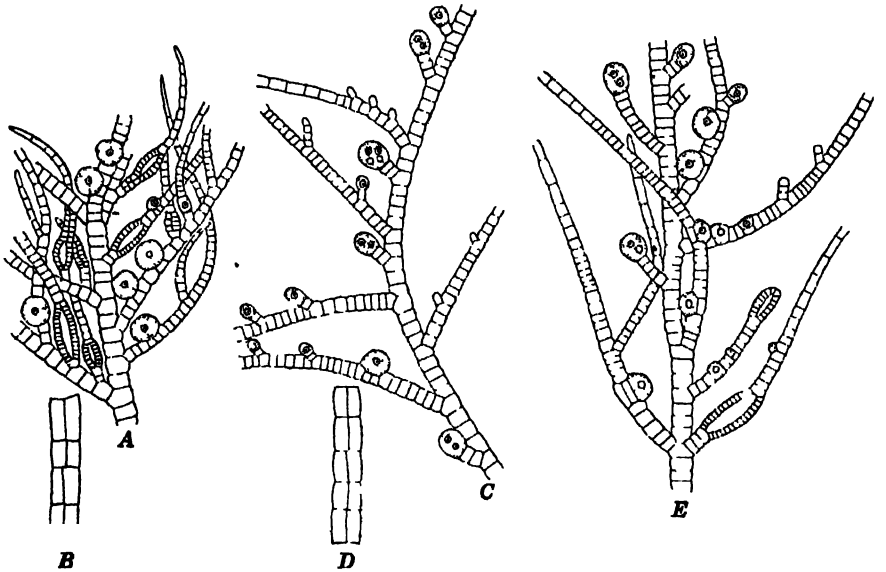


FIG. 129.—*Haplospora globosa* Kjellm. *A B*, upper and lower portions of a gametophyte. *C–D*, upper and lower portions of a sporophyte. *E*, upper portion of a sporophyte bearing both unilocular and neutral sporangia. (*After Brebner*, 1896.) (*A–C*, × 100; *D–E*, × 75)

protoplast into uninucleate spores (Fig. 130*D*). The monospore escapes through a large pore at the distal end of the sporangial wall.[2] A germinating spore sends forth a long germ tube, and then it divides into uninucleate cells.[3]

The alga known as *Scaphospora speciosa* Kjellm. (Fig. 129*A*) is vegetatively identical with *H. globosa*. It bears two kinds of reproductive organs; an intercalary unicellular organ producing a single large, uninucleate, nonflagellated, aplanospore-like body (Fig. 130*C*), and an intercalary multicellular organ in which each cell produces a single biflagellate zooid (Fig. 130*B*). Gametic union of the zooid and the

[1] Nienburg, 1923; Dammann, 1930.
[2] Reinke, 1889. [3] Nienburg, 1923.

nonflagellated body has not been demonstrated, but there is a strong presumption that the two are, respectively, an antherozoid and an egg.

Several phycologists[1] hold that *Haplospora globosa* and *Scaphospora speciosa* are alternate generations of the same species, and they call that species *H. globosa* because this name has priority. One reason for considering "*Scaphosphora*" the gametophyte of *Haplospora* is the identity of their vegetative structures. A stronger reason is the occasional production of the *Scaphospora*-type of reproductive organs upon thalli of *Haplospora* (Fig. 129*E*). In addition to terminal unilocular sporangia with quadrinucleate protoplasts, the sporophyte of *Haplospora* may bear intercalary, one-celled, uninucleate organs[2] comparable to oogonia of *Scaphospora*, or it may bear both kinds of *Scaphospora* organs.[3] The *Scaphospora*-like organs upon sporophytes of *Haplospora* have been

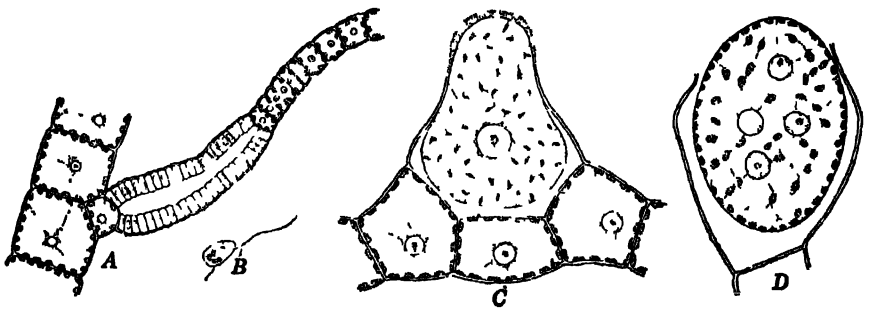


FIG. 130.—*Haplospora globosa* Kjellm. *A*, antheridium. *B*, antherozoid. *C*, oogonium. *D*, unilocular sporangium. (*After Reinke*, 1889.) (*A*, × 150, *B*, × 600, *C–D*, × 300.)

called "antheridia" and "oogonia," but it is much more probable that their nuclei are diploid and that their homologies lie with neutral sporangia of other Phaeophyta. According to their structure, neutral sporangia of *Haplospora* produce a single large neutral aplanospore or many small neutral zoospores.

ORDER 4. CUTLERIALES

The Cutleriales have a flattened, blade- or disk-like thallus in which growth is entirely or partially trichothallic. The sporophytes produce unilocular sporangia only. The gametophytes are heterothallic and markedly anisogamous.

There are but two genera. One (*Zanardinia*) has an alternation of identical generations; the other (*Cutleria*) has an alternation of somewhat different ones. However, the two genera seem closely related, because they have several distinctive features in common, including a unique

[1] Brebner, 1896; Kylin, 1917, 1933; Oltmanns, 1922; Reinke, 1889.
[2] Brebner, 1896; Reinke, 1889. [3] Brebner, 1896

method of trichothallic growth, a unilocular sporangia with a small number of large zoospores, and similar anisogamous sex organs.

Cutleria is found in the Mediterranean and along the coast of Europe where the water is warm. The sporophyte of one species is known from Florida and the West Indies. The gametophyte is an erect flattened blade with numerous irregular dichotomies (Fig. 131*A*). Growth takes place at the upper margin of a blade where there are many erect uniseriate hairs. Each hair has an intercalary growing region, and

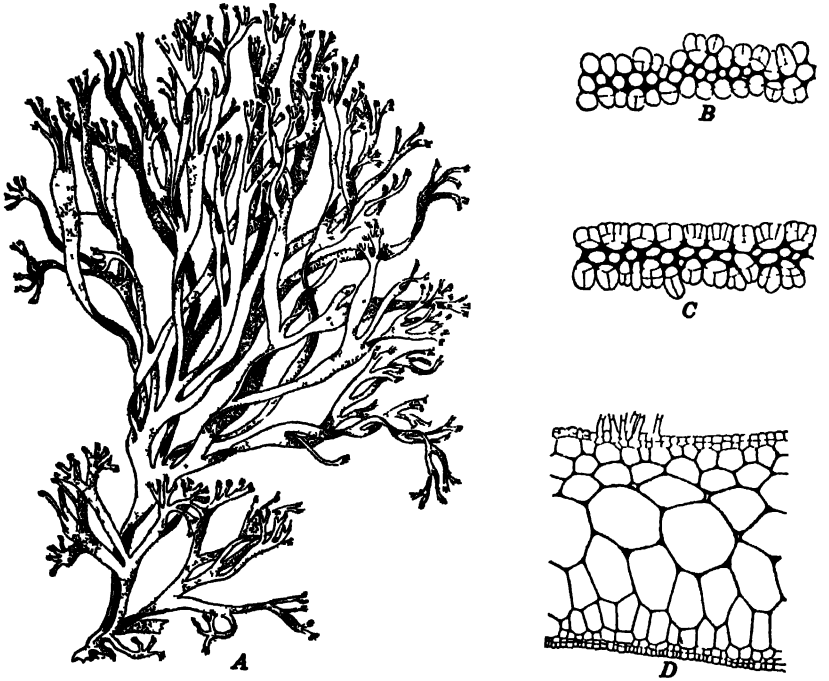


FIG. 131.—*A*, gametophyte of *Cutleria multifida* Grev. *B–D*, successive transverse sections of apex of gametophyte of *C. adspersa* DeNot (*A*, *after Thuret, in Oltmanns*, 1922; *B–D*, *from Sauvageau*, 1899.) (*A*, × ½; *B–C*, × 150, *D*, × 75.)

cells posterior to the growing region divide in a vertical plane. Multiseriate portions of the hairs abut on one another and lie compacted in a more or less homogeneous parenchymatous mass.[1] With maturation of these cells, there is a differentiation into an epidermis-like layer one or two cells in thickness, an underlying cortex-like layer of much larger isodiametric cells, and an axial group of vertically elongate cells (Fig. 131*B–D*).

Gametophytes of *Cutleria* are heterothallic and have the sex organs developing in small or large clusters upon both flattened surfaces of the thallus. A superficial epidermal cell may develop directly into a

[1] Sauvageau, 1899.

male gametangium, or it may develop into a branched hair which bears several gametangia (Fig. 132*A*). A fertile cell first divides transversely into a *primary stalk cell* and an *antheridial initial.* The primary stalk cell may remain undivided, or it may divide transversely to form a vertical row or two or more stalk cells. Transverse division of the antheridial initial and of its daughter cells produces a row of four or five cells. Further division may be in a vertical or in a transverse

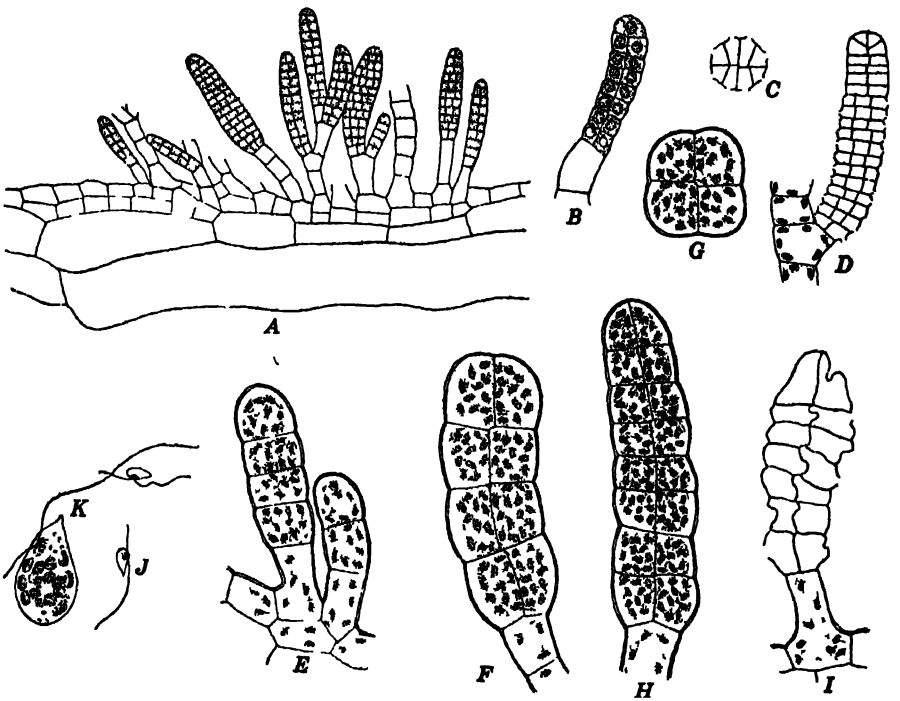


FIG. 132.—*Cutleria multifida* Grev. *A*, vertical section through a male sorus. *B*, a young male gametangium *C–D*, transverse and vertical sections of empty male gametangia *E–H*, stages in development of female gametangia *I*, an empty female gametangium *J*, male gametes *K*, female gamete. (*J–K*, *after Kuckuck*, 1929.) (*A*, × 325, *B–I*, × 650, *J–K*, × 500.)

plane. Division continues[1] until the fertile portion is 20 or more tiers in height and with each tier composed of eight cells (Fig. 132*B*). The protoplast of each cell is then metamorphosed into a biflagellate male gamete which escapes through a pore into the free face of the wall enclosing it (Fig. 132*C–D*).

The sequence of development in a female gametangium is similar, except for the production of a much smaller number of cells (Fig. 132*E–I*). Female gametangia are but four to seven tiers in height, with only four

[1] Yamanouchi, 1912.

cells in each tier.[1] Each female gamete also escapes through a pore in the surrounding wall.

Free-swimming male gametes are pyriform and with a single reddish chromatophore at the point of flagellar insertion (Fig. 132*J*). Free-swimming female gametes (Fig. 132*K*) are also pyriform, but they contain a dozen or more chromatophores.[2] At the time of gametic union the male gametes are actively motile, and the female are sluggish or immobile. Fusion of the two gamete nuclei follows within a few hours, and the

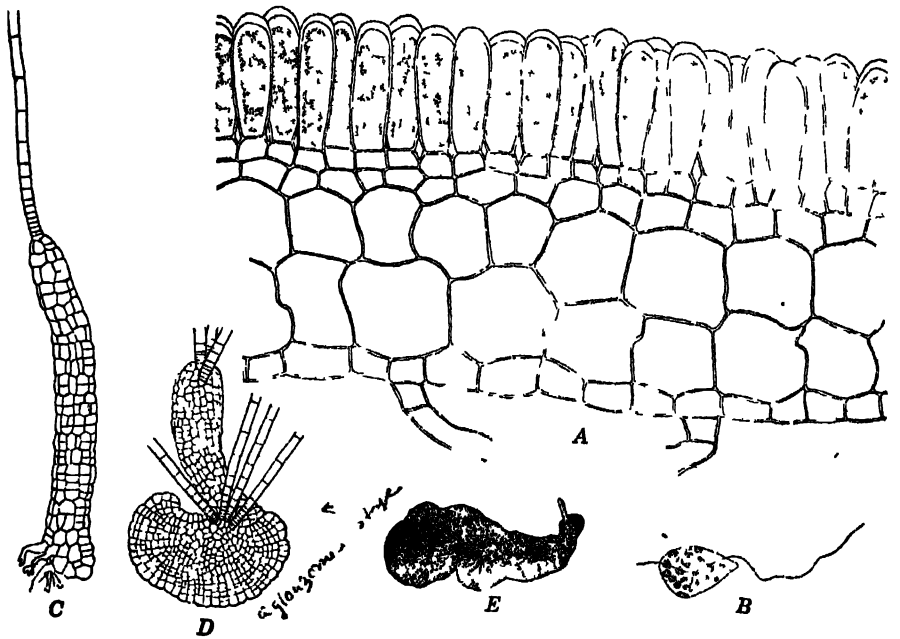


FIG. 133.—*A–B*, *Cutleria multifida* Grev. *A*, vertical section through a fertile portion of a sporophyte. *B*, zoospore. *C–E*, *C. adspersa* DeNot. *C*, *D* young sporophytes. *E*, old sporophyte. (*B*, *after Kuckuck*, 1899, *C–E*, *from Sauvageau*, 1899.) (*A*, × 325, *B*, × 650; *C*, × 100; *D*, × 75; *E*, × 9.)

zygote begins to develop into a sporophyte within a day.[1] Unfertilized female gametes develop parthenogenetically into gametophytes.

The sporophyte of *Cutleria* was first described as a separate genus (*Aglazonia*). Although germlings from zygotes of *Cutleria* and from zoospores of *Aglozonia* have not been grown to maturity in culture, they have been grown to a sufficiently advanced stage to show[3] that the two are alternate generations of each other. At first, growth of a young sporophyte is trichothallic and vertically upward into a columnar structure (Fig. 133*C*). Upward growth ceases when the plant is about 10 days old, and all further growth is laterally outward from the base

[1] Yamanouchi, 1912. [2] Kuckuck, 1929; Yamanouchi, 1912.
[3] Falkenburg, 1879; Church, 1898; Sauvageau, 1899; Yamanouchi, 1912

of the column. Repeated cell division at the base of the column produces a flat, disk-like tissue[1] which expands laterally as a result of division and redivision of the marginal cells (Fig. 133*D–E*).[1] The sporophyte is homologous with a minute gametophyte subtended by an extraordinarily enlarged, fertile holdfast. The prostrate "holdfast" of the sporophyte, which constitutes almost all the thallus, is several cells in thickness and has the outermost cells differentiated into an epidermis-like layer. It is attached to the substratum by numerous multicellular rhizoids growing out from ventral epidermal cells.

The unilocular sporangia are arranged in a palisade-like manner in sori borne upon the dorsal surface of a thallus (Fig. 133*A*). Each sporangium is developed from a single epidermal cell. This fertile cell divides transversely into a primary stalk cell and a sporangial initial. The primary stalk cell may remain undivided, or it may divide to form as many as six stalk cells; the sporangial initial develops directly into a sporangium. The single nucleus of the initial divides reductionally,[2] and simultaneous nuclear division continues until there are 8, 16, or 32 nuclei. There is then a cleavage into uninucleate protoplasts, each of which is metamorphosed into a large pyriform, biflagellate zoospore with several chromatophores (Fig. 133*B*). The zoospores escape through a large apical pore in the sporangial wall. After swarming 10 to 90 minutes, they become quiescent, round up, and secrete a wall. This cell divides and redivides to form a typical young gametophyte.[2]

The longevity of the two generations has been followed at Plymouth, England,[3] and at Naples.[4] The sporophyte is perennial and fruits in winter or spring. The gametophyte is a spring annual which disappears during the summer.

ORDER 5. DICTYOTALES

The Dictyotales have an erect, flattened, parenchymatous thallus in which growth is initiated by a single apical cell or by a marginal row of apical cells. Both generations are identical. Unilocular sporangia of the sporophyte each produce four or eight large aplanospores. The gametophytes are oogamous.

There are some 18 genera and 100 species. The Dictyotales are characteristic of temperate and tropical seas but occur in greatest abundance in the warmer waters of the tropics. On the Atlantic Coast of the United States, Dictyotales are found from Beaufort, North Carolina, southward; on the Pacific Coast they range southward from Santa Barbara, California.

[1] Sauvageau, 1899; Yamanouchi, 1912. [2] Yamanouchi, 1912.
[3] Church, 1898. [4] Funk, 1927.

The Dictyotales are frequently considered quite distinct from other Phaeophyta because the diploid asexual generation produces non-flagellated spores. In *Dictyota* and most other genera the spores are produced in fours. Because of this, they are sometimes called *tetraspores*. This name is misleading, both because it implies a relationship with tetraspore-forming Rhodophyceae and because it obscures the fact that sporangia of Dictyotales are in reality unilocular sporangia. The eight-spored sporangium of *Zonaria* (Fig. 135*G*) is evidently a unilocular

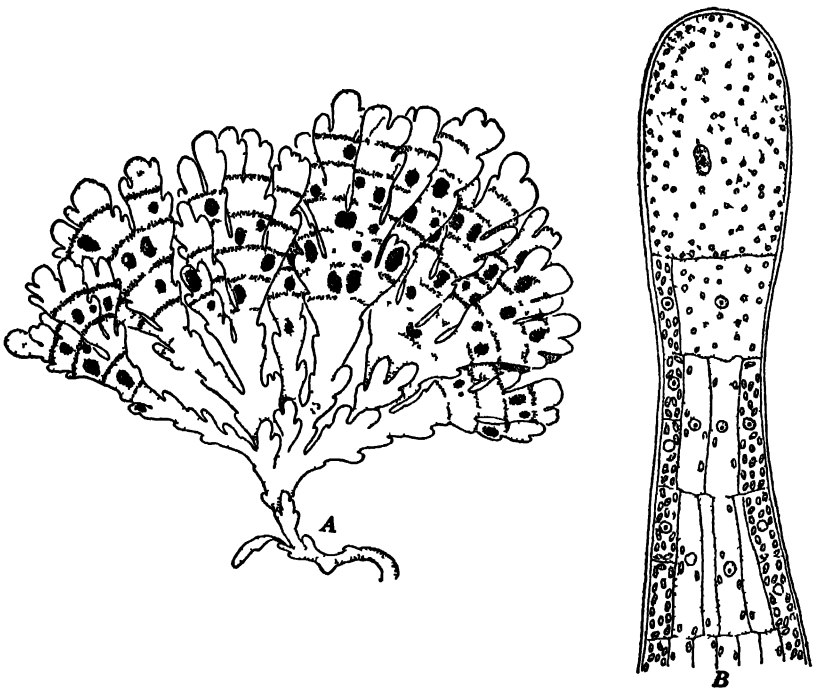


FIG 134.—*Zonaria Farlowii* Setchell and Gardner *A*, female gametophyte *B*, thallus apex in vertical section (*A*, × ½, *B*, × 325)

sporangium. The lack of flagella, although striking, is not a matter of deep significance. The homologies between antheridia of Dictyotales and typical gametangia of other Phaeophyta are obvious. So, also, are those between oogonia and typical gametangia, if the oogonium is interpreted as a many-celled gametangium which does not develop beyond the one-celled stage.

Zonaria is found along both shores of this country. Its gametophyte and sporophyte are identical in appearance and distinguishable from each other only when in fruit. The thallus of *Z. Farlowii* Setchell and Gardner, a Pacific Coast species, is fan-shaped, 8 to 15 cm. in height, and grows attached to rocks by a disk-shaped holdfast (Fig. 134*A*) The

erect portion is differentiated into a vertical stalk and numerous flattened blades, all in approximately the same plane. Growth of the thallus is at the upper margin and is due to a continuous marginal row of apical cells. Branching of the blades results from the death of a few adjoining apical cells and a continuation of growth by apical cells lateral to them.

There is usually a simultaneous transverse division of all apical cells of a blade segment. Each derivative cut off from an apical cell divides vertically and in a plane parallel to the thallus surface.[1] The first two divisions cut off a flat, primary, epidermal initial toward either face of the thallus (Fig. 134*B*). An epidermal initial usually divides anticlinally to form four quadrately disposed epidermal cells, each containing many small discoform chromatophores. Meanwhile the large central cell divides and redivides vertically in the same plane to form six daughter cells. Thus, as a rule, mature portions of a thallus are eight cells in thickness. Now and then all epidermal cells in a transverse belt equidistant from the thallus margin develop into multicellular unbranched hairs. These hairs persist for a long time and lie in parallel transverse rows across one or both sides of the thallus.

Reproductive organs, both sexual and asexual, are produced in irregular sori which lie between the transverse bands of hairs (Fig. 134*A*). Both generations of *Z. Farlowii* are perennials and both fruit at all seasons of the year. However, there are indications[1] that reproduction, especially of the sporophyte, is cyclic instead of continuous and that it occurs twice each lunar month and during the spring tides.

The gametophytes are heterothallic. Each antheridium in a sorus of a male plant is developed from a superficial thallus cell a short distance back from the apex. This cell divides transversely into a primary stalk cell, which does not divide, and into an antheridial initial (Fig. 135*A*). The antheridial initial divides transversely to form a filament of four or five cells, after which division is both vertical and transverse. The end product of these divisions is an antheridium 20 to 40 tiers in height and one with 8 or 16 small cubical cells in each tier (Fig. 135*B*). Upon the cessation of cell division, there is a rounding up of the protoplasts and a gelatinization of the walls between them. As a result,[1] the entire sorus becomes a gelatinous matrix in which there are numerous irregularly distributed, rounded protoplasts (Fig. 135*C*). There is then a metamorphosis of the protoplasts into antherozoids. The structure of antherozoids of *Zonaria* is unknown, but those of *Dictyota* have been found[2] to be pyriform and with one (?) laterally inserted flagellum.

Oögonial sori differ from antheridial sori in that only certain superficial cells of a fertile region develop into sex organs (Fig. 135*D*). Each fertile cell elongates vertically and then divides transversely into a

[1] Haupt, 1932. [2] Williams, 1904*A*.

primary stalk cell and a primary oogonial cell, neither of which divide. The primary oogonial cell increases greatly in size and becomes a large oogonium that contains a single egg (Fig. 135*E*). Eventually there is a gelatinization of the oogonial wall [1] Liberation of eggs has not been observed in *Zonaria*, but there is every reason for supposing it similar

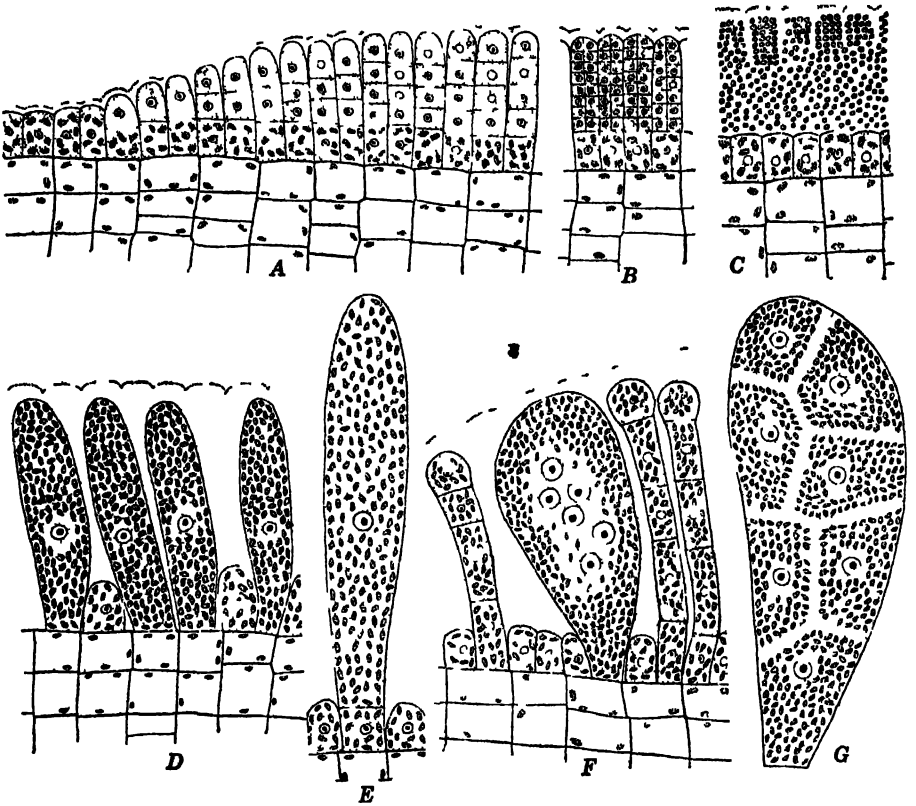


FIG 135 —*Zonaria Farlowii* Setchell and Gardner *A C*, vertical sections of male sori with antheridia at various stages of development *D*, vertical section through a portion of a young female sorus *E*, mature oogonium *F* vertical section through a portion of a young sorus of a sporophyte *G*, mature unilocular sporangium (× 325)

to that of *Dictyota*,[2] where the eggs escape from the gelatinous matrix and are fertilized while floating about in the water.

Sori of the sporophyte have certain of the superficial cells developing into sporangia and the remaining ones developing into sterile hairs (*paraphyses*) four to six cells long (Fig. 135*F*). Sporangial development from a fertile cell is direct and without any formation of a stalk cell. The sporangium enlarges to many times its original size Its single nucleus divides reductionally,[1] and each of the four haploid nuclei

[1] Haupt, 1932 [2] Williams, 1904*A*.

divides equationally. There is then a cleavage of the octonucleate protoplast into eight large uninucleate aplanospores (Fig. 135*G*) which are liberated by a rupture of the sporangial wall.

CLASS 2. HETEROGENERATAE

The Heterogeneratae have a life cycle in which the two alternating generations are unlike in vegetative structure. The sporophyte is always the larger of the two, and it is generally of macroscopic size and definite form. The gametophyte is microscopic. In fact, knowledge concerning the gametophytes of all members of the class has only been obtained by growing them in cultures started with zoospores from unilocular sporangia. Sporophytes of Heterogeneratae may produce either zoospores or neutral spores. Reproduction of the gametophyte may be isogamous or oogamous.

According to vegetative structure of the sporophyte, the Heterogeneratae are divided into the two following subclasses:

Haplostichineae in which growth is trichothallic and in which the thallus is built up of one or more filaments and their branches.

Polystichineae in which growth is not trichothallic and in which longitudinal and transverse intercalary cell division produces a parenchymatous thallus.

Possibly, for reasons to be given on a later page (page 255), this segregation into Haplostichineae and Polystichineae is artificial and not natural.

SUBCLASS 1. HAPLOSTICHINEAE

Sporophytes of Haplostichineae are trichothallic and composed of filaments which may be free from one another, interwoven with one another, or so densely compacted that the thallus seems to be parenchymatous. A sporophyte may produce either zoospores or neutral spores. The gametophytes are always microscopic and either isogamous or oogamous.

The subclass is divided[1] into three orders.

ORDER 1. CHORDARIALES

The Chordariales include those Haplostichineae in which the branched filamentous sporophyte is not markedly compacted into a pseudoparenchymatous thallus. Thus far, all known gametophytes are isogamous.

The order includes at least three families.[1] Those who classify Phaeophyta according to the structure of reproductive organs place all[2] or most[3] of the Chordariales in the Ectocarpales.

[1] Kylin, 1933; Taylor, 1936. [2] Oltmanns, 1922.
[3] Setchell and Gardner, 1925.

Myrionema, a genus with several species, has a minute thallus which grows epiphytically upon various other algae. Opinion is divided as to whether it is a primitive small plant or a small reduced form of a more advanced type. *M. strangulans* Grev., the only species that has been studied in culture,[1] grows epiphytically upon *Ulva*. It is found along both coasts of this country.

The thallus appears to be a parenchymatous disk when it is viewed from above, but in reality it consists of radiately branched horizontal filaments laterally apposed to one another. Growth of the horizontal filaments is terminal or subterminal. Each cell inward from the growing tip cuts off a daughter cell toward its free (upper) surface. Most of the daughter cells develop into erect unbranched filaments four to six cells tall or into erect unbranched hairs with many more cells (Fig. 136*A*).

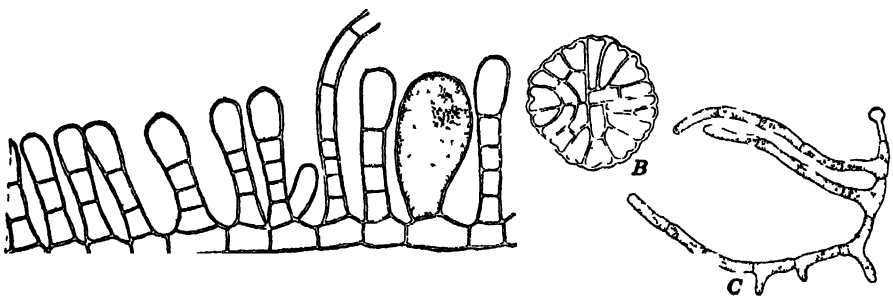


FIG. 136.—*Myrionema strangulans* Grev. *A*, vertical section through a mature sporophyte. *B*, surface view of a young sporophyte. *C*, gametophyte. (*B–C, after Kylin*, 1934.) (*A*, × 650; *B*, × 400; *C*, 375.)

Other of the daughter cells develop into unilocular or into plurilocular reproductive organs. The first reproductive organs formed by the thallus are usually plurilocular. They are several cells in height, uniseriate, and with each cell producing a typical zooid. The zooid grows into a thallus identical with that producing it (Fig. 136*B*) and one which bears either unilocular or plurilocular organs.[1] Thus *Myrionema* is a sporophytic generation in which there may be a reduplication of the sporophyte by neutral spores from multicellular neutral sporangia.

Old sporophytes usually bear unilocular sporangia only (Fig. 136*A*). Zoospores from these sporangia germinate to form branched filamentous thalli[1] in which the branches are free from one another as in *Ectocarpus*. It is thought that the filamentous plants (Fig. 136*C*) are gametophytes, but as yet none of them have been grown to a mature fruiting condition. The fact that neutral spores develop into typical *Myrionema* thalli makes it very improbable that the *Ectocarpus*-like plants developing from zoospores of unilocular sporangia are cultural monstrosities.

[1] Kylin, 1934.

Leathesia is another of the Chordariales found along both coasts of this country. It is a common alga of the midlittoral zone. *L. difformis* (L.) Aresch, is an annual which appears early in spring, reaches its maximum size in midsummer, and begins to degenerate early in the fall. Mature thalli are irregularly globose, with a much convoluted surface, generally hollow at the center, and up to 8 cm. in diameter (Fig. 137). Solid portions of a thallus have a gelatinous fleshy texture. The solid portion consists of a radiating mass of di- or trichotomously branched filaments, with more or less gelatinous material between the branches (Fig. 138*A*). The lowermost cells of the branches (those toward the thallus center) are irregularly cylindrical and colorless. Cells toward the tips of branches are progressively smaller. Most of the branches terminate in palisade-like branchlets four or five cells long, but here and there they

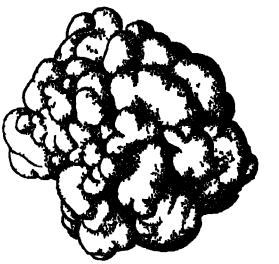


FIG. 137.—Sporophyte of *Leathesia amplissima* Setchell and Gardner ($\times \frac{1}{2}$).

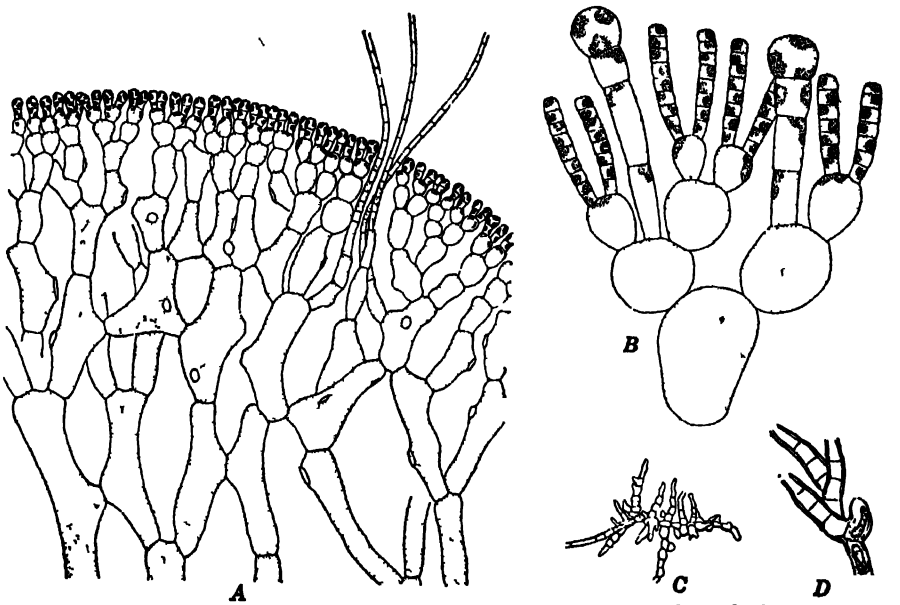


FIG. 138.—*Leathesia difformis* (L.) Aresch. *A*, vertical section through the outer portion of a sporophyte *B*, outer portion of a sporophyte, bearing neutral sporangia. *C*, gametophyte. *D*, empty gametangia. (*C–D*, *from Dammann*, 1930) (*A*, × 120, *B*, × 485, *C*, × 155; *D*, × 430)

terminate in a cluster of long multicellular hairs. Cells of the palisade-like branchlets are the only ones with chromatophores.

L. difformis may produce either unilocular or plurilocular reproductive organs, or both. This shows that it is a sporophyte. Fruiting generally

begins with a formation of unilocular sporangia. Sooner or later there is a formation of neutral sporangia, and these are frequently the only reproductive organs present on old thalli (Fig. 138*B*). The neutral spores are undoubtedly diploid, and it has been shown[1] that they develop into *Leathesia* plants which bear neutral sporangia. Neutral spores may also develop into small *Myrionema*-like plants which produce neutral sporangia.[2] These are considered plethysmothalli[3] rather than precociously fruiting thalli. One of the reasons for considering them distinct from juvenile stages of typical thalli is the presence of but one chromatophore in each cell, instead of several as in cells of adult plants.[4]

The gametophyte generation (Fig. 138*C–D*) is but imperfectly known. Cultures started from zoospores in midsummer contained minute branched thalli which remained small and did not fruit until the following June.[5]

At that time they produced plurilocular reproductive organs. The gametangial nature of these organs was not definitely established because liberation of zooids and their fusion were not observed. Within a month after fruiting, there was a development of a new crop of microscopic plants bearing plurilocular organs. Before the end of December, these gave rise successively to six generations, each with plurilocular organs. It is not improbable that the first slowly developing generation was a gametophyte and the six succeeding ones were diploid (plethysmothallic?) and reproduced by means of neutral spores.

ORDER 2. SPOROCHNALES

The Sporochnales have a sporophyte in which each branch terminates in a tuft of hairs. Growth is trichothallic and due to intercalary cell division at the base of each hair. The unilocular sporangia are usually borne terminally and in dense clusters. The gametophyte is microscopic and oögamous.

There are 6 genera and about 25 species. They are found in warm and temperate seas, especially in the waters of the Australian region. Two species of one genus (*Sporochnus*) are found on the Atlantic Coast of this country from Beaufort, North Carolina, southward.[6]

Carpomitra, with some five species, is found along the Atlantic Coast of Europe. Its sporophyte, which may be 30 cm. or more in height, is a flattened cylinder with several successive dichotomous branchings (Fig. 139*A*). Each branch has an evident midrib, and at each branch tip there is a conspicuous tuft of hairs. Growth of a branch apex is trichothallic, the meristematic region being situated in a group of cells at the base of the terminal tuft of hairs. The tissue formed posterior to the

[1] Kylin, 1933. [2] Sauvageau, 1925. [3] Sauvageau, 1928, 1932.
[4] Sauvageau, 1932. [5] Dammann, 1930. [6] Hoyt, 1920; Taylor, 1928.

meristem is solidly parenchymatous. It is differentiated into a medullary region with vertically elongated cells and a cortical region with approximately isodiametric cells.

Sporophytes produce only unilocular sporangia. At the time of reproduction there is a development of a miter-like inflation, the *receptacle*, immediately below the tuft of hairs terminating a fertile branch (Fig. 139*B*). Many of the superficial receptacular cells develop into branched fertile hairs (paraphyses).[1] The sporangia develop from ter-

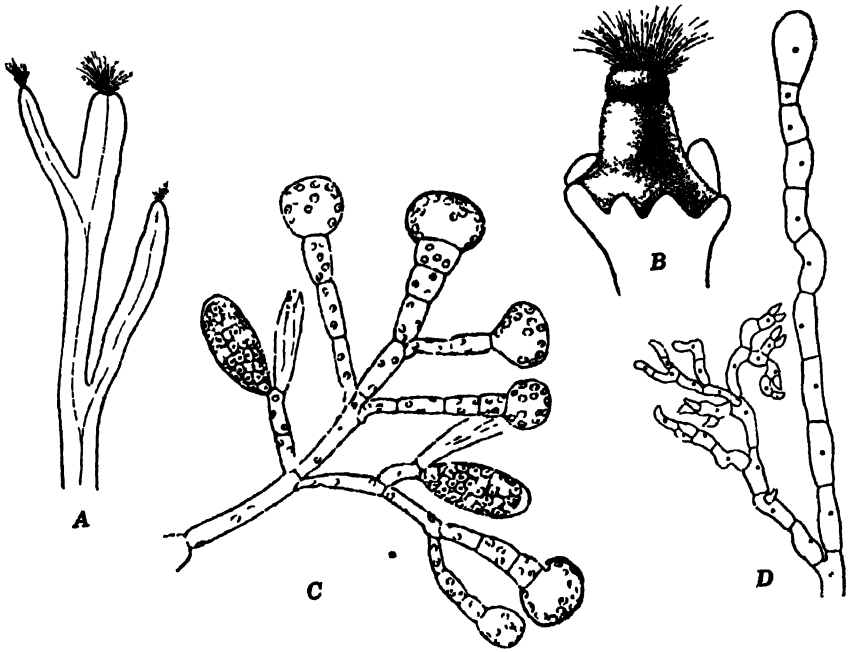


FIG. 139.—*Carpomitra cabrerae* Kutz. *A*, upper portion of sporophyte. *B*, apex of sporophyte. *C*, fertile paraphysis from a sporophyte apex *D*, gametophyte. (*From Sauvageau*, 1926.) (*A*, × 3½, *B*, × 15, *C*, × 480, *D*, × 330.)

minal cells of a paraphysis. They are ovoid and contain a relatively small number of zoospores (Fig. 139*C*).

Germinating zoospores[2] develop into a uniseriate, sparingly branched, filamentous gametophytes (Fig. 139*D*). The antheridia are produced at the tips of short lateral branchlets. Their size and shape are much the same as in *Laminaria*. Antherozoids have never been observed, but the discovery of many empty antheridia upon the gametophyte indicates that there is a liberation of motile male gametes. The oögonia are large, ovoid, and develop from terminal or intercalary cells of the main branches. The oögonial nature of the cells interpreted as oögonia

[1] Johnson, 1891; Sauvageau, 1926. [2] Sauvageau, 1926.

is not established beyond all doubt because there is neither an extrusion of an egg nor a development of a pore in the oögonial wall. Instead, there is a direct division and redivision of the oögonial cell to form the new sporophyte. This parthenogenetic germination of the egg differs from other known cases of parthenogenesis in that the germinating egg does not become invested with a wall distinct from the oögonial wall.

The young sporophyte develops into an erect, unbranched, uniseriate filament 20 or more cells tall (Fig. 140*A–B*). Following this there is a horizontal division of the sixth to eighth cell below the apex. The

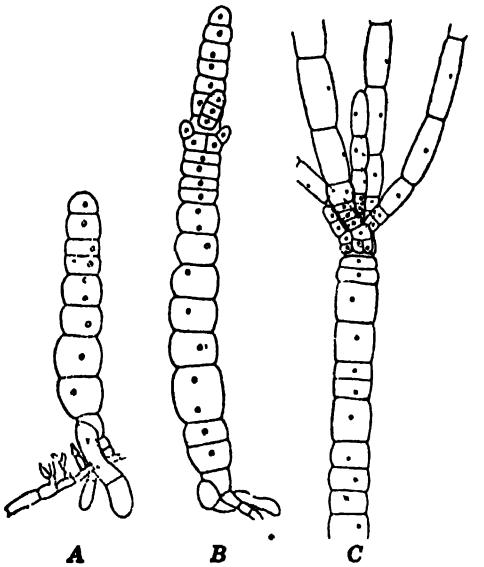


FIG. 140.—*Carpomitra cabrerae* Kutz. Stages in development of young sporophytes. (*From Sauvageau*, 1926.) (*A–B*, × 180, *C*, × 120.)

superior daughter cell divides vertically to form initials which develop into hairs; the inferior daughter cell divides vertically to form a meristem which begins to form tissues similar to those of an adult thallus (Fig. 140*C*). Further growth is similar to that at any branch tip of a mature sporophyte.

ORDER 3. DESMARESTIALES

Thalli of Desmarestiales have a single filament at each growing apex. Posterior to this there is a pseudoparenchymatous cortication of the filament to form a thallus of definite macroscopic form. The gametophyte is microscopic, oögamous, and has the discharged egg remaining attached to the oögonial apex.

The order contains but three genera.

Desmarestia has two centers of distribution, namely, north Atlantic and north Pacific waters as contrasted with Antarctic and adjoining

regions. There are two or three species along the Atlantic Coast of this country and about eight along the Pacific Coast. Most of them grow below the low-tide mark. *Desmarestia* is one of the larger brown algae, and certain species, as *D. latissima* Setchell and Gardner, attain a length of more than 5 meters. Several of the species differ from other brown algae in that they accumulate malic acid in abundance; the cell sap of certain species growing along the coast of California has a pH of 2.



FIG 141.—Upper portion of sporophyte of *Desmarestia herbacea* (Turn.) Lamx. (natural size)

The thallus, the sporophyte, grows attached to rocks by means of a disk-like hold'ast. Above this is an axis of variable length and one which may be sparingly or profusely branched. The branches of an axis may be subcylindrical or they may be flattened into conspicuous blades (Fig. 141). Blades of the largest species along the Pacific Coast (*D. latissima*) are sometimes more than 2.5 meters long and 20 cm. broad.

The growing apex of each branch terminates in an axial filament in which the cells are joined end to end in a single row. The axial filament bears many lateral, unbranched, uniseriate filaments, all in the same plane and either in opposite pairs (Fig 142*A*) or alternate with one another. Growth of axial and lateral filaments is due to an intercalary meristematic region. The lowermost cells of lateral filaments, three or four back from the growing zone of the central axis, send out multicellular

rhizoidal outgrowths that become closely applied to the axial filament. Repeated cell division in this ensheathing layer eventually produces a corticating tissue several cells in thickness and one in which the superficial cells may continue division indefinitely (Fig. 142*B*). There is generally a disappearance of lateral filaments along the corticated

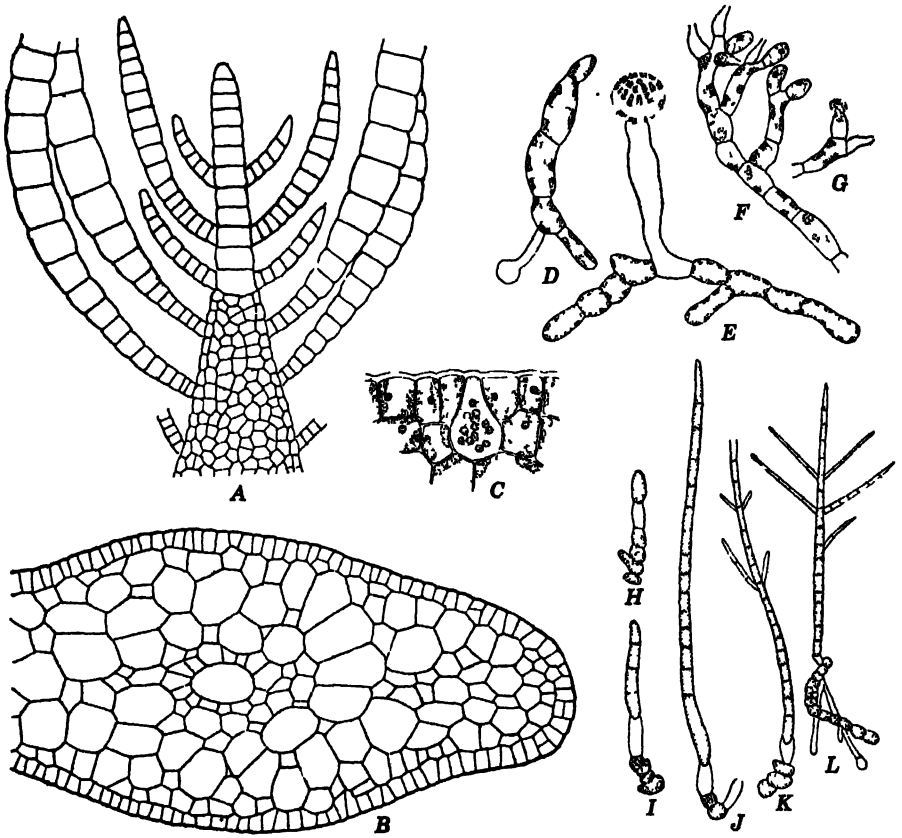


FIG. 142.—*A–C*, sporophyte of *Desmarestia herbacea* (Turn.) Lamx. *A*, surface view of growing apex. *B*, transverse section of corticated portion. *C*, unilocular sporangium. *D–L*, *D. aculeata* (L.) Lamx. *D–E*, female gametophytes. *F*, male gametophyte. *G*, liberation of antherozoid. *H–L*, early stages in development of sporophytes. (*D–L*, *after Schreiber*, 1932.) (*A*, × 215; *B*, × 160; *C*, × 650.)

portion of an axial filament, but now and then one of them continues growth as an axial filament by sending out lateral filaments and becoming corticated. Many of the plants that one collects lack axial filaments at their branch apices. This may have been due to an abscission or to an accidental breaking off of the filament. In either case there is no further apical growth of the blade.

Unilocular sporangia are the only reproductive organs formed by a sporophyte. They may be developed from epidermal cells of the

corticated portion or from cells of an axial filament or its appendages.[1] Unilocular sporangia on the corticated portion are of the same size and shape as epidermal cells. They lie embedded in the thallus and scattered over the entire blade (Fig. 142*C*). The protoplast of a sporangium becomes divided into 25 to 50 (32 or 64?) zoospores, and there is every reason for supposing that there is a reduction division of the original diploid nucleus.

The zoospores have two laterally inserted flagella of unequal length. The zoospores swarm for an hour or more, then they lose their flagella, come to rest, and secrete a wall. This cell soon sends forth a germ tube, and most of the protoplasm migrates into its somewhat swollen tip.[2] The tip becomes partitioned off by a transverse wall, and the cell thus cut off develops into a microscopic, sparingly branched gametophyte of 20 to 40 cells. Vegetative male and female gametophytes may be distinguished from each other because cells of a male plant are about half the diameter of those of female ones (Fig. 142*F–G*). Male gametophytes are also composed of more cells and are more freely branched than are female gametophytes. Antheridia are developed in clusters and at the tips of lateral branchlets. Each antheridium is one-celled, and its protoplast is metamorphosed into a single antherozoid. A female gametophyte may begin to form oogonia at the three- or four-celled stage, or it may not begin to form them until it is many-celled (Fig. 142*D–E*). In either case, the oogonia are developed by a vertical enlargement of an intercalary cell. An oogonium contains a single large egg which is extruded through, but remains attached to, the apex of the oögonial wall.

Fertilization has not been observed, but it is very probable that it does take place. The zygote, assuming that there is a gametic union, secretes a wall and elongates vertically.[2] It divides transversely, and repeated division in the same plane produces a long, erect, unbranched filament of 15 or more cells which remains attached to the oögonial apex (Fig. 142*H–J*). Lateral branches then grow outward from the upper cells of the filament, and rhizoidal branches grow downward from the lowermost cells (Fig. 142*K–L*). The gametophyte disappears shortly after the young sporophyte develops rhizoids. The branched upper portion of the sporophyte continues trichothallic growth and soon becomes corticated in exactly the same manner as the growing apex of a mature plant.

Gametophytes of *Desmarestia* and the Laminariales have several unique features in common. These include clusters of unicellular antheridia, vertically elongated intercalary oögonia, attachment of the extruded egg to the oögonial apex, and growth of the young sporophyte upon the oögonial apex. Because of this, the Demarestiales and Lami-

[1] Johnson, 1891; Kuckuck, 1894. [2] Schreiber, 1932.

nariales have been thought to be rather closely related to each other.[1] If they are related, the segregation of the Heterogeneratae into Haplostichineae and Polystichineae is artificial since it makes the Desmarestiales and Laminariales each the culmination of an independent series.

SUBCLASS 2. POLYSTICHINEAE

Sporophytes of Polystichineae have a parenchymatous thallus produced by vertical and transverse division of intercalary cells. A sporophyte may produce either zoospores or neutral spores. The gametophytes are always microscopic and isogamous, anisogamous, or oögamous.

The subclass is divided[2] into three orders.

ORDER 1. PUNCTARIALES

The Punctariales are a somewhat ill-defined assemblage in which the sporophyte is of medium size, parenchymatous, without marked internal differentiation of tissues, and grows by intercalary cell division. The reproductive organs may or may not be in definite sori. Sporophytes may produce either zoospores or neutral spores. The gametophytes are microscopic and either isogamous or anisogamous.

The order includes at least three families.[3]

Soranthera is the first member of the order known to have an alternate microscopic gametophyte.[4] It is found only in the Pacific Ocean. There is but one species, *S. ulvoidea* Post. and Rupr. It grows epiphytically upon *Rhodomela* and is a common alga of the midlittoral zone along the entire Pacific Coast of this country. Mature thalli are subspherical, hollow, and up to 7 cm. in diameter (Fig. 143*A*). The solid portion consists of a superficial epidermis-like layer of small cells and an underlying layer four or five cells in thickness which is composed of much larger cells. Chromatophores are restricted to the superficial cell layer.

Unilocular sporangia, the only reproductive organs produced by the sporophyte, are borne in sori about 1 mm. in diameter. The sori are irregularly distributed over the entire surface of the thallus. Soral development begins with a periclinal division of each cell in a future fertile area. Repeated transverse division of each outer daughter cell produces an erect unbranched filament (paraphysis) 10 to 20 cells long. Cells toward the exterior of paraphyses are rounded and contain chromatophores (Fig. 143*B*). Certain of the inner daughter cells of the original epidermal cells cut off a cell which develops into a unilocular sporangium. The paraphyses serve as a protective covering for the sporangia during the time thalli are exposed by the receded tide. The sporangia discharge

[1] Schreiber, 1932. [2] Kylin, 1933; Taylor, 1936.
[3] Kylin, 1933. [4] Angst, 1926.

their zoospores in a mass through a small pore at the sporangial apex when the thallus is reflooded by the incoming tide The zoospores remain motionless for a few seconds after discharge and then swim freely in all directions

Development of a mature fruiting gametophyte from a zoospore may be completed within three weeks [1] The gametophyte is an irregularly branched *Ectocarpus*-like filament of 50 or more cells (Fig 143*C*) The gametangia are borne at the tips of one- or two-celled lateral branchlets

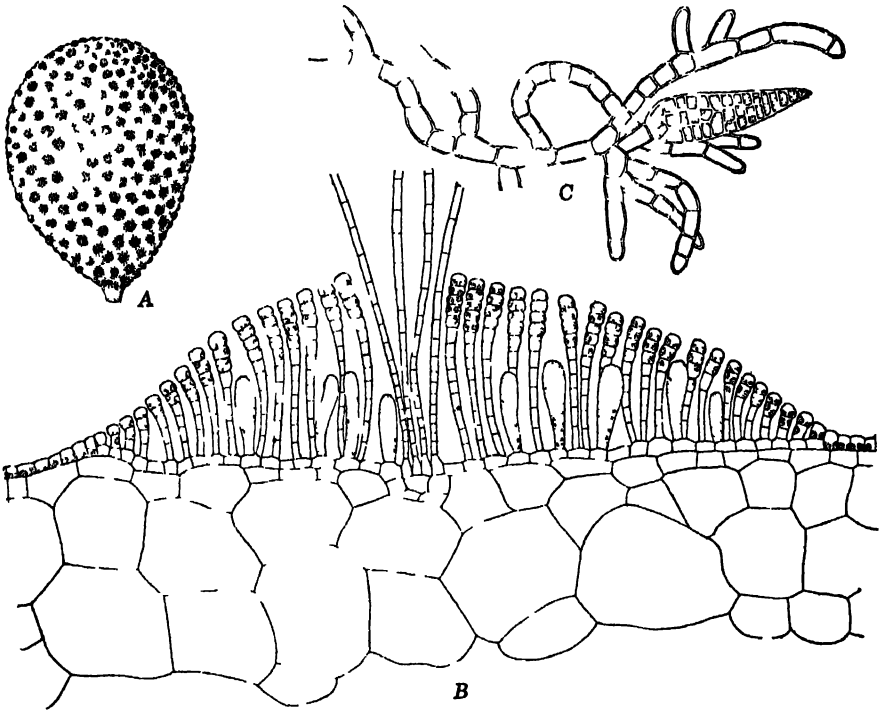


Fig 143 *Scaithera ulvella* Post and Ruprecht *A* sporophyte *B* vertical section through a sorus of a sporophyte *C* gametophyte (*C after Angst* 1926) (*A* natural size *B* × 160 (*C* × 280)

They are 15 to 20 tiers in height and with several cells in each of the median tiers Gametic union is anisogamous[1] and with a small active male gamete uniting with a larger, more sluggish one Development of the zygote into a sporophyte has not been studied experimentally.

ORDER 2 DICTYOSIPHONALES

The Dictyosiphonales have profusely branched cylindrical thalli in which growth is initiated by a single apical cell Mature portions of a thallus are internally differentiated into two or into three regions The

[1] Angst, 1926

sporophytes usually produce unilocular sporangia only. The gametophytes are microscopic and isogamous.

There is but one family, the *Dictyosiphonaceae*, with some 4 genera and 15 species

Dictyosiphon is found in cold waters along both coasts of this country. *D. foeniculaceus* (Huds) Grev , the commonest species, is a summer

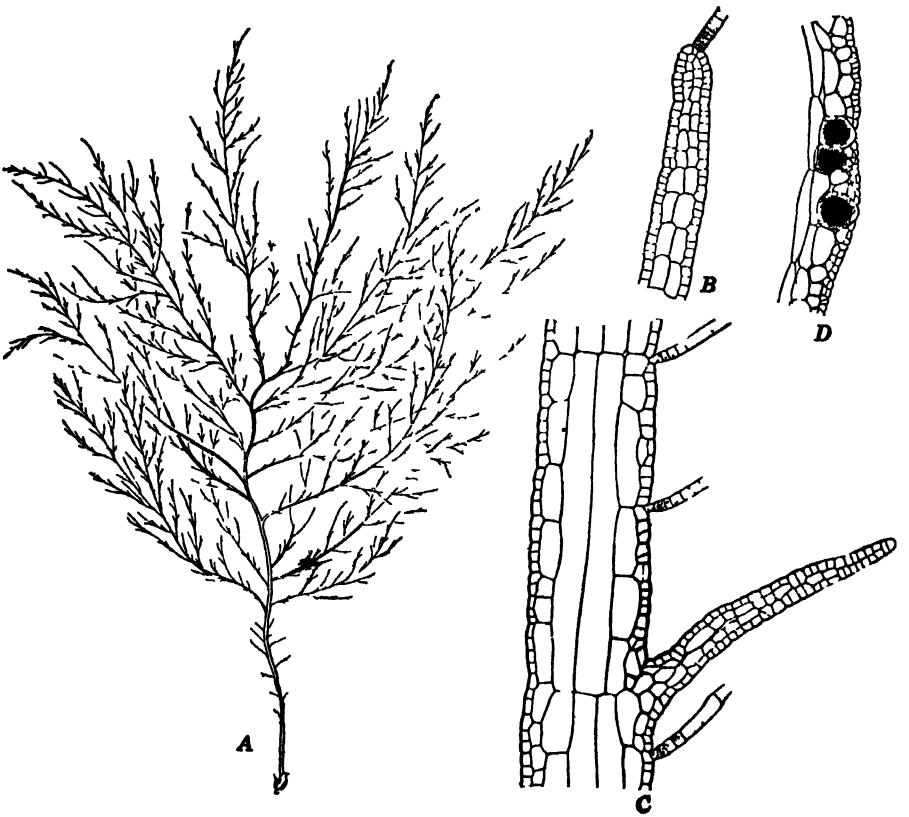


FIG 144 —*A–C*, *Dictyosiphon foeniculaceus* (Huds) Kutz *A* sporophyte *B*, branch apex of a sporophyte *C*, vertical section through mature region of a sporophyte *D*, unilocular sporangia of *D Macounii* Farl (*B D, from Kuckuck*, 1929) (*A*, × ½, *B–C*, × 150, *D*, × 100)

annual which grows in the midlittoral zone Its thread-like cylindrical thallus is freely branched and with the ultimate branchlets tapering to an acute point (Fig 144*A*) Each branch tip has a single apical cell which persists as long as growth continues, after which[1] it may be replaced by a hair (Fig 144*B*).

Mature portions of a thallus may be solid or hollow (Fig. 144*C*). Solid portions have a central core of vertically elongated colorless cells

[1] Kuckuck in Oltmanns, 1922.

surrounded by an ensheathing layer of small isodiametric cells containing chromatophores. Certain of the superficial cells develop into long unbranched hairs.

The unilocular sporangia, which are larger than adjoining vegetative cells (Fig. 144*D*), lie embedded just beneath the thallus surface. The sporangia are formed by enlargement of isodiametric cells next to the axial core of elongated cells.

The zoospores, which are of the usual phaeophycean type, germinate immediately to form branched filamentous *Ectocarpus*-like gametophytes.[1] The gametangia are uniseriate, 2 to 12 cells in height, and with each cell producing a single motile gamete. Germination of the zygote follows immediately after conjugation. Gametes that have failed to conjugate round up, secrete a wall, and germinate parthenogenetically. A germinating zygote develops into a filamentous protonema-like diplonema. Later on, certain cells of the filamentous diplonema develop into an upright columnar structure closely resembling the growing apex of an adult sporophyte.[1]

ORDER 3. LAMINARIALES

Most members of the Laminariales (the kelps) have a sporophyte externally differentiated into holdfast, stipe, and blade. Growth is due to an intercalary meristematic region, and it usually lies between stipe and blade. Mature regions anterior and posterior to the meristem are internally differentiated into three concentric tissues. The sporophytes produce unilocular sporangia only, which lie in extensive sori borne upon the blade. Several genera have the sori restricted to special blades (*sporophylls*). The gametophytes are microscopic and oogamous.

The order includes about 30 genera and 100 species. They are inhabitants of the colder waters of the globe. Kelps do not grow in tropical regions nor in temperate regions except where the water is cool. In polar regions they extend as far up as there is a suitable bottom free from permanent or nearly permanent ice. Most of the kelps grow below the low-tide line. There are four genera of the Laminariales along the Atlantic Coast of this country. Eighteen genera are found along the Pacific Coast, and 14 of them are known only from the Pacific Ocean. Many of the Pacific Coast kelps are notable both for their size and for their external complexity of form. The most striking of these are the "giant kelps" which grow in water 10 to 30 meters in depth. The commonest giant kelp of the West Coast, *Macrocystis pyrifera* (L.) Ag. (Fig. 154*A*) has a repeatedly branched stipe 30 to 50 meters long. There is a continuous formation of new blades at the branch tips. Mature blades are borne at regular intervals along a branch, and each of them has

[1] Sauvageau, 1917.

a pear-shaped gas bladder at its base. *Nereocystis Luetkeana* (Mert.) Post and Rupr. (Fig. 145*B*), another common Pacific Coast giant kelp, is an annual. It has an unbranched stipe 20 to 25 meters long and one that terminates in a single large gas bladder. Above the bladder are numerous short dichotomously forked branches, each terminating in a single blade 3 to 4.5 meters long. The "sea palm," *Postelsia palmaeformis* Rupr. (Fig. 146), is the most striking of the smaller kelps. It grows in the midlittoral zone, but only on rocky headlands exposed to

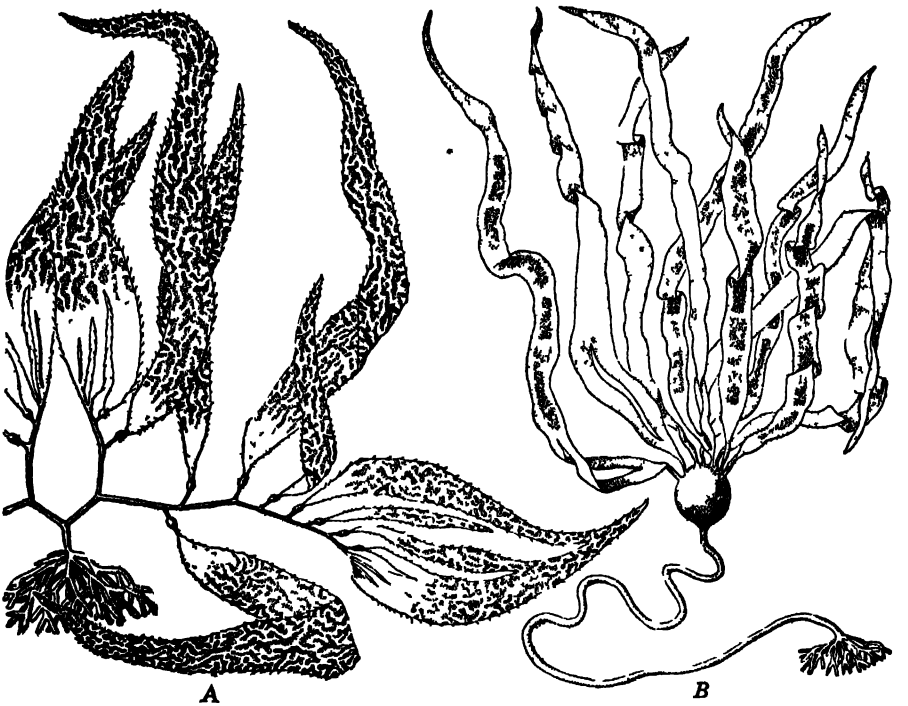


FIG. 145.—*A*, *Macrocystis pyrifera* (L.) Ag. *B*, *Nereocystis Luetkeana* (Mert.) Post and Rupr. (*A*, × 1/12, *B*, × 1/20)

the full pounding of the surf. It has a stout flexible stipe, about half a meter long, with numerous short dichotomies at the distal end, each terminating in a narrow blade

At one time the kelps, together with the rockweeds (Fucales), were the chief source of potassium and iodine. The discovery of mineral deposits containing these elements has made their recovery from algae unprofitable for the past 80 years. There was a commercial recovery of these elements from Pacific Coast kelps during the World War, but this ceased when the European supply again became available.

Kombu, a product made from various kelps, enters into the diet of almost every Japanese family and is one of the standard foods of the

country. Recent statistics are not available, but in the decade 1892 to 1901 the production of dried kelp averaged more than 28,000 tons a year and averaged more than $426,000 in value.[1] The kelps are harvested from July to October by fishermen who go out to kelp beds in boats. The plants are gathered by means of hooks attached to poles or by means of hooked dredges. Harvested kelps are spread out on the shore to dry, and the rough-dried plants are then sent to manufacturers for conversion into kombu. Upon arriving at a factory, the plants are boiled a few minutes in fresh water and then allowed to dry until the surface is no longer wet. They are then spread out one by one in flat wooden presses, and the whole mass is compressed as tightly as possible. The compressed mass is then reduced to shreds by means of a hand plane, the cutting being done lengthwise along the edges of the parallel blades. Kombu is also prepared by soaking the plants in vinegar and shredding them one by one.



Fig. 146.—*Postelsia palmiaeformis* Rupr. (× ¼)

Laminaria, the genus after which the order is named, is found along both coasts of this country. Most of the species are perennial, but at least one of them (*L. ephemera* Setchell) is an annual. The plant body is differentiated into three distinct parts; holdfast, stipe, and blade (Fig. 147*A*). The holdfast may be a solid disk or a system of forked root-like branches (*hapteres*). The stipe is always unbranched and either cylindrical or somewhat flattened. The blade may be simple or vertically incised into a number of segments, and its surface may be smooth or much convoluted.

Growth of the sporophyte is due to an intercalary meristem at the juncture of stipe and blade. Meristematic activity results in a continuous increase in length of the stipe. On the other hand, the length of a mature blade remains approximately constant because increase in length at the base about equals abrasion at the apex.[2] Blades of most species persist for but one year. They stop growing late in the summer and begin to disintegrate in the autumn after the plant has discharged its zoospores. As the blade begins to disintegrate, there is an elongation of the axial portion of the meristem below it.[2] This causes a transverse

[1] Smith, H. M., 1905. [2] Setchell, 1905.

rupture of the cortical portion of the meristem. The exposed axial portion becomes flattened as it increases in length, and, as growth continues, it becomes distinctly blade-like (Fig. 147*B–C*). The old blade may persist for a time upon the apex of the new intercalated blade, but eventually there is an abrasion of the old blade.

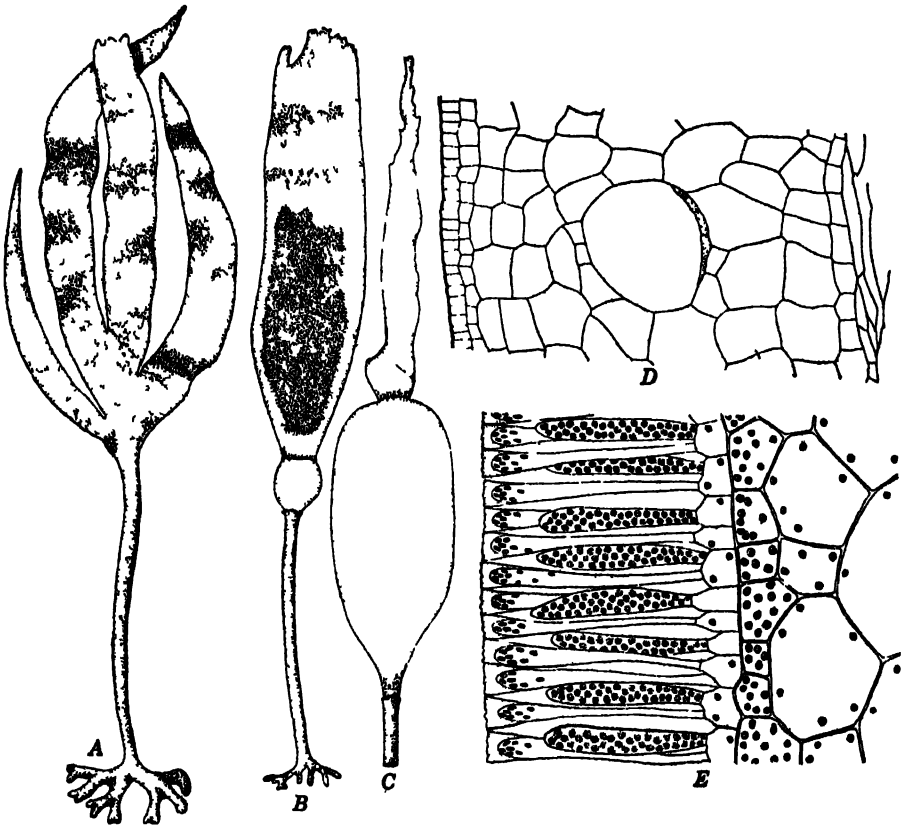


FIG. 147.—*A–C*, *Laminaria Andersonii* Farlow *A*, sporophyte *B–C*, stages in the regeneration of new blades *D E*, *L Farlowii* Setchell *D*, transverse section of portion of a blade containing a mucilage canal *E*, transverse section through a portion of a sorus (*A*, × ¼; *B–C*, × ½, *D*, × 215, *E*, × 485)

The stipe is differentiated into a central axis (*medulla*), cortex, and epidermis, each containing distinctive elements. However, the transition from one region to another is gradual, not abrupt. The medulla of young stipes and the meristematic medulla of older ones consist of vertical, parallel, unbranched filaments ("hyphae") which lie close to one another. In slightly more mature medullae the vertical filaments lie a short distance from one another (Fig. 148*A–E*) Certain cells of a filament divide diagonally to cut off initial cells of *connecting filaments* and the apposed

initials elongate laterally until they meet each other.[1] Many of the connecting filaments become several cells in length through repeated transverse division. The many-celled connecting filaments tend to run horizontally across the medulla, but many of them run diagonally because of unequal elongation of the vertical filaments to which they are attached. Elongation of certain of the vertical filaments is accompanied by cell division, so that they remain composed of relatively short cells. In other filaments there is but little division, and the cells become long

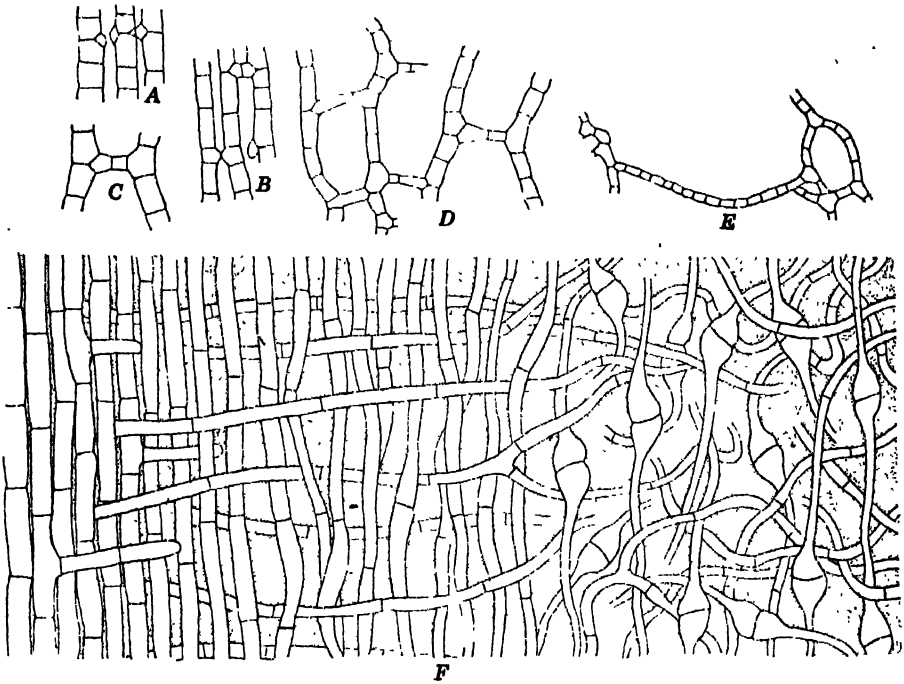


FIG. 148.—*A–E*, vertical sections through the embryonic region showing early stages in development of medullary tissue in stipe of *Laminaria digitata* (Turn.) Lamx. *F*, diagrammatic longitudinal section through medulla of stipe of *L. Andersonii* Farlow. Outer region at the left, inner at the right. (*F*, × 215.) (*A–E*, *after Killian*, 1911.)

(Fig. 148*F*). These filaments have been called *trumpet hyphae*[2] because of their greater breadth near the transverse walls. The nature of the trumpet hyphae is a matter of dispute, but there is considerable evidence[3] showing that they are rather like the sieve tubes of vascular plants. There are numerous pores in the transverse walls between adjoining cells; the adjoining protoplasts are connected by strands of cytoplasm extending through the pores. The trumpet hyphae also resemble sieve tubes in that perforated portions of the end walls (the *sieve plates*) become blocked off by callus pads when they become old. Microchemical

[1] Killian, 1911. [2] Oliver, 1887. [3] Oliver, 1887; Sykes, 1908.

studies on sieve tubes of *Nereocystis* indicate[1] that they contain soluble proteins which tend to accumulate near the sieve plates, often more on one side than the other. This suggests that the sieve tubes may function in the transport of foods.

The cortex is formed by division and redivision of superficial cells of a young stipe. It is composed of more or less radially arranged, vertically elongated cells. There is a continuous increase in diameter at the periphery of the cortex as long as the plant remains alive. Cells formed at the end of a growing season are smaller than those formed early in the season. Because of this, the cortex contains one or more concentric rings resembling the annual rings in the secondary wood of a dicotyledonous stem. Cortices of many species contain *mucilage ducts*, either just beneath the epidermis or just outside the medulla. They are an anastomosing system of canals filled with mucilage. The mucilage is produced by groups of secretory cells at the inner face of a duct.[2]

The epidermis is one or two cells in thickness and composed of small cubical cells containing many chromatophores.

The internal structure of a blade resembles that of a stipe. At the center is a flattened medulla with vertical and connecting filaments. External to the medulla is a cortex composed of isodiametric cells that are progressively smaller toward the epidermis (Fig. 147*D*). Several species have mucilage ducts in their cortices. The epidermis is usually but one cell in thickness. Both it and the outermost cortical cells contain numerous chromatophores.

Unilocular sporangia, which are the only reproductive organs produced by the sporophyte, are generally formed at a specific season, either summer or autumn. They are borne in extensive sori nearly covering both surfaces of a blade (Fig. 147*B*). Each epidermal cell of a young soral area sends forth a finger-like outgrowth at its outer face. A transverse wall is formed at the base of the outgrowth, and the cell thus cut off elongates to form an erect unicellular paraphysis with a conspicuous cap of gelatinous material at the apex (Fig. 147*E*). Formation of the palisade-like layer of paraphyses is followed by a cutting off of a unilocular sporangium at the outer face of what was formerly an epidermal cell. The sporangia become club-shaped and about two-thirds as long as the paraphyses. The single nucleus of a young sporangium divides meiotically, and simultaneous nuclear division continues until there are 32 or 64 nuclei. There is then a cleavage into uninucleate protoplasts and a metamorphosis of them into zoospores.

Sporophytes growing in the intertidal zone discharge their zoospores at the time of reflooding by the incoming tide. The mass of zoospores discharged from a sporangium is enclosed by a watery gelatinous sheath

[1] Rigg, 1925. [2] Guignard, 1892.

as it exudes between the paraphyses, and the sheath persists for a minute or more after extrusion beyond them. Then the sheath dissolves, and the zoospores swim freely in all directions.

Zoospores round up, after swarming for a time, secrete a wall, and soon send forth a germ tube. The nucleus and chromatophores move into the germ-tube apex, and a transverse wall is formed posterior to them. This cell develops into the cellular gametophyte.[1] In *L. saccharina* (L.)

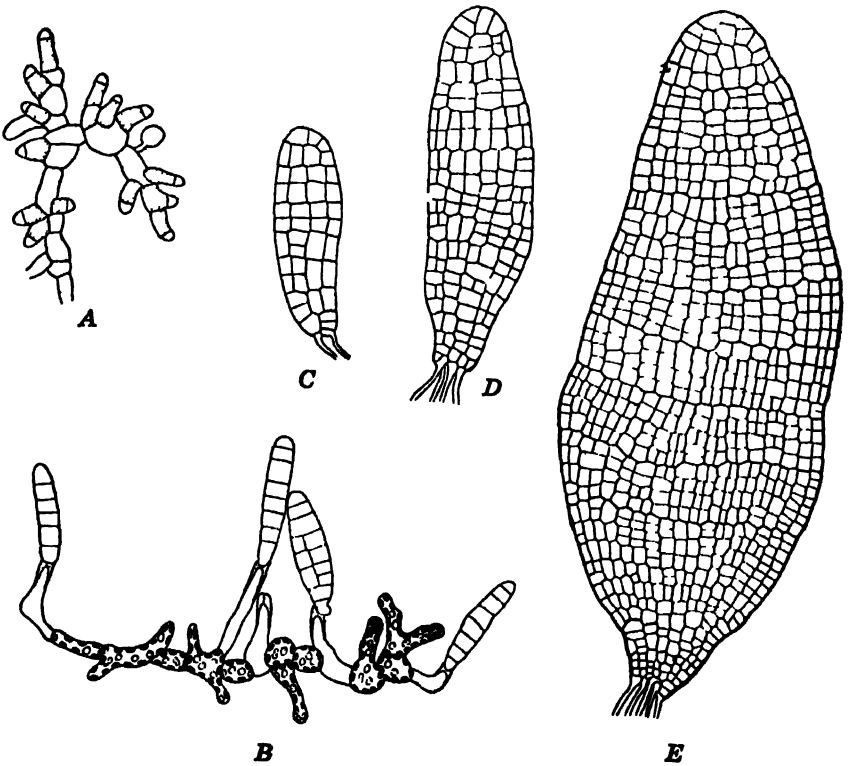


FIG. 149.—*Laminaria flexicaulis* Le Jol. *A*, male gametophyte. *B* female gametophyte with young sporophytes. *C*–*E*, somewhat later stages in development of sporophyte. (*From Sauvageau*, 1918.) (*A*, × 480, *B*–*E*, × 180.)

Lamx. there is a genotypic determination of sex during the reduction division. Half of the 32 zoospores develop into male gametophytes and half into female gametophytes.[2] Both male and female gametophytes may begin a production of sex organs after they are two or three cells in length, but the male gametophytes usually become many-celled before they fruit. Fruiting is directly dependent upon temperature, and it has been shown[2] that gametophytes remain vegetative if the temperature of the culture is above 15°C. Sterile gametophytes may be distinguished

[1] Kylin, 1916; Myers, 1926; Sauvageau, 1918. [2] Schreiber, 1930.

from each other because cells of female gametophytes are twice the diameter of those of male plants. Many-celled male gametophytes produce antheridia in abundance and at the tips of one- or two-celled lateral branches (Fig. 149*A*). Each antheridium is one-celled, and its protoplast is metamorphosed into a single antherozoid with two lateral flagella. Oögonia of female gametophytes are developed from both intercalary and terminal cells. In either case, the oögonium elongates vertically, and its protoplast develops into a single egg. The egg is extruded through, but remains attached to, a pore at the apex of the oögonial wall (Fig. 149*B*).

An antherozoid swims to and fuses with the egg attached to the oögonial apex. Union of gametes is followed by a union of their nuclei.[1] Soon after this, the zygote begins to develop into a sporophyte. By successive transverse divisions it develops into a vertical row of 6 to 10 cells. Median cells of the row then divide vertically, and this is soon followed by a vertical division of all cells but the lowermost.[2] The lowermost cell elongates to form a rhizoid in much the same manner as a root hair grows out from an epidermal cell of a root of a vascular plant.[3] Continued division in two planes produces an expanded blade-like sheet, one cell in thickness but with several hundred cells (Fig. 149*C E*). Additional rhizoids are developed from the lowermost cells of the blade, and the gametophyte disappears after three or four rhizoids have been produced. Eventually cells in the lowermost portion of the blade divide in a third plane, producing a meristematic region comparable to that of an adult sporophyte. The upper face of this meristem contributes to the blade, the lower face gives off derivatives that mature into a stipe.

CLASS 3. CYCLOSPOREAE

The Cyclosporeae have a life cycle in which there is no alternation of generations. The plant body is a sporophyte, and spores produced by the unilocular sporangia function as gametes. Gametic union is always of an oögamous type. The thallus is always parenchymatous and with growth initiated by a single apical cell. The sporangia are borne within special cavities (*conceptacles*). Conceptacles may be scattered over the whole surface of a thallus, but more frequently they are limited to inflated tips of branches (*receptacles*).

There is but one order, the Fucales. It contains some 32 genera and 325 species. These are generally placed in a single family, the Fucaceae.

The Fucales are world wide in distribution, but those of Arctic and North Temperate seas differ considerably from those of Antarctic and South Temperate waters. There are also characteristic genera in the

[1] Williams, 1921. [2] Kylin, 1916; Myers, 1926; Sauvageau, 1918.
[3] Sauvageau, 1918.

intervening tropical zone Most of the Fucales grow permanently attached to rocks, but in some cases, as in certain species of *Sargassum*, the thallus is free-floating Thalli of species growing in the intertidal zone are rarely over a meter in length; those of certain species growing below the low-tide level may become more than 5 meters long.

The sporangial nature of the so-called sex organs of Fucales has already been discussed (page 227). All Fucales are heterosporous; with *macrosporangia* ("oogonia") producing large aplanospores ("eggs") and with

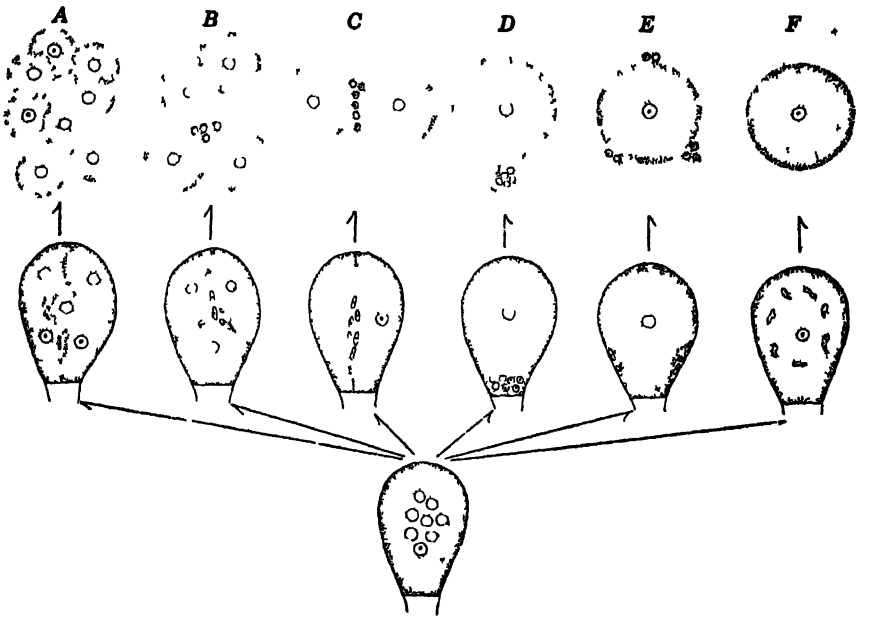


FIG 150.—Diagrams showing the development of the various types of macrosporangia found among the Fucales *A Fucus* type *B Ascophyllum* type *C, Pelvetia* type *D, Hesperophycus* type *E Cystoseira* type *F Sargassum* type

microsporangia ("antheridia") producing small zoospores ("antherozoids") A sporophyte may be monoecious or dioecious

Development of microsporangia is identical with that of unilocular sporangia, and there is generally a production of 64 zoospores The zoospores differ from those of other Phaeophyta in that the posterior flagellum is the longer of the two.[1]

Developing macrosporangia have a reduction division of the nucleus and an equational division into eight nuclei. The subsequent development (Fig. 150) is according to one of the following types: (1) the *Fucus* type[2] in which there is a cleavage into eight uninucleate aplanospores; (2) the *Ascophyllum* type[3] in which four uninucleate spores are formed and four supernumerary nuclei are extruded between them; (3) the

[1] Kylin, 1916*A*, 1920 [2] Farmer and Williams, 1898 [3] Oltmanns, 1889.

Pelvitia type[1] with two uninucleate spores and six supernumerary nuclei; (4) the *Hesperophycus* type[2] with one large uninucleate spore and a small basal seven-nucleate spore; (5) the *Cystoseira* type[2] in which seven nuclei are extruded; and (6) the *Sargassum* type[3] in which all but one of the

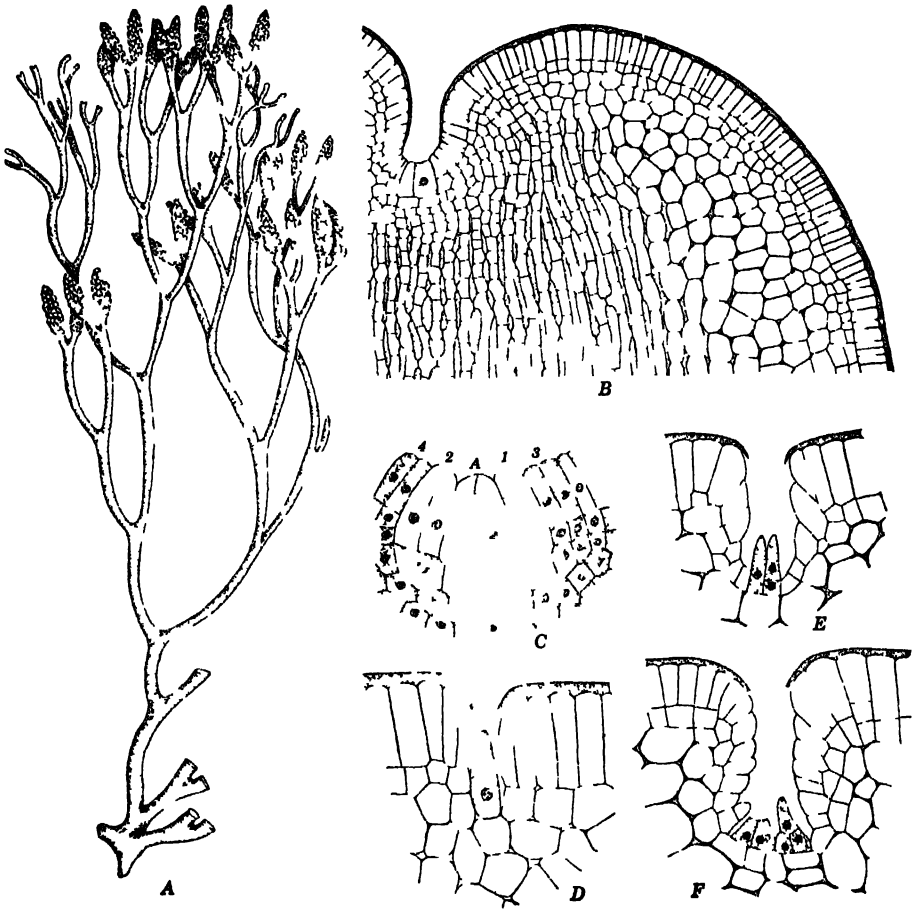


FIG 151.—*Pelvetia fastigiata* (J G Ag) DeToni *A* thallus *B*, semidiagrammatic longitudinal section of a thallus apex *C*, apical cell and recently formed derivatives Successively formed derivatives are numbered consecutively *D F*, early stages in development of conceptacles (*A*, × ½, *B*, × 160, *C*, *E F*, × 325, *D*, × 485)

nuclei degenerate before or after gametic union. The *Fucus* type appears to be the most primitive and the others modifications of it.

Most of the Fucales found along the shores of this country grow high in the intertidal zone. *Fucus*, described in almost every textbook of general botany, is found along both coasts of this country. *Pelvetia*, here selected to exemplify the Fucales, grows in profusion in the upper

[1] Oltmanns, 1889 [2] Gardner, 1910 [3] Nienburg, 1910; Tahara, 1913.

littoral zone along the entire Pacific Coast of the United States and along the shores of Europe.

The thallus of the Pacific Coast species, *P. fastigiata* (J.G.Ag.) DeToni, is 20 to 40 cm. tall and attached by a disk-shaped holdfast. The erect portion of the thallus is a somewhat flattened cylinder with many dichotomous branchings (Fig. 151*A*). Each branch tip has a single four-sided pyramidal apical cell which cuts off segments laterally and basally (Fig. 151*C*). The first division of lateral segments is periclinal. The outer daughter cells divide and redivide to form the parenchymatous cortical tissue of mature regions. The inner daughter cells, together with derivatives from the basal face of the apical cell, divide to form cells that mature into a medulla composed of parallel longitudinal filaments laterally separated from one another by gelatinous material (Fig. 151*B*). Occasionally an apical cell divides vertically into two daughter cells, each of which becomes an apical cell. Growth initiated by the pair of apical cells produces a new dichotomy of the branch.

P. fastigiata is a perennial and fruits throughout the year. The sporangia (sex organs) are formed within conceptacles borne upon somewhat inflated tips of branches (receptacles) Each conceptacle is derived from a single superficial cell which lies close to the growing apex.[1] The conceptacular initial lies slightly below the level of adjoining vegetative cells (Fig. 151*D*). It divides vertically, and both daughter cells divide transversely (Fig. 151*E*). The two outer cells remain undivided; the two inner divide and redivide to form an expanded sheet, the *fertile layer*, two or three cells in thickness (Figs 151*F*, 152*A*). It is the layer lining the flask-shaped open cavity (the conceptacle), resulting from continued division and enlargement of cells lateral to the conceptacular initial. A mature conceptacle (Fig. 152*B*) is globose and with a relatively small opening, the *ostiole*. Superficial cells of the fertile layer may produce sterile hairs (paraphyses) or sporangia. Paraphyses are developed from fertile-layer cells immediately inward from the ostiole. A paraphysis is several cells in length, unbranched, and with terminal cell vertically divided. The paraphyses project through the ostiole and a very short distance beyond it.

Microsporangia (antheridia) develop directly from cells of the fertile layer or at the bases of fertile paraphyses growing out from them (Fig. 153*G–H*). It is very probable that, as is certainly known in other Fucales,[2] division of the primary nucleus of a microsporangium is reductional. Simultaneous nuclear division continues until there are 64 nuclei in a microsporangium; then there is a cleavage into 64 zooids.

Certain cells in the lower portion of a fertile layer function as initials of macrosporangia (oögonia). A macrosporangial initial divides trans-

[1] Moore, 1928; Nienburg, 1913. [2] Yamanouchi, 1909.

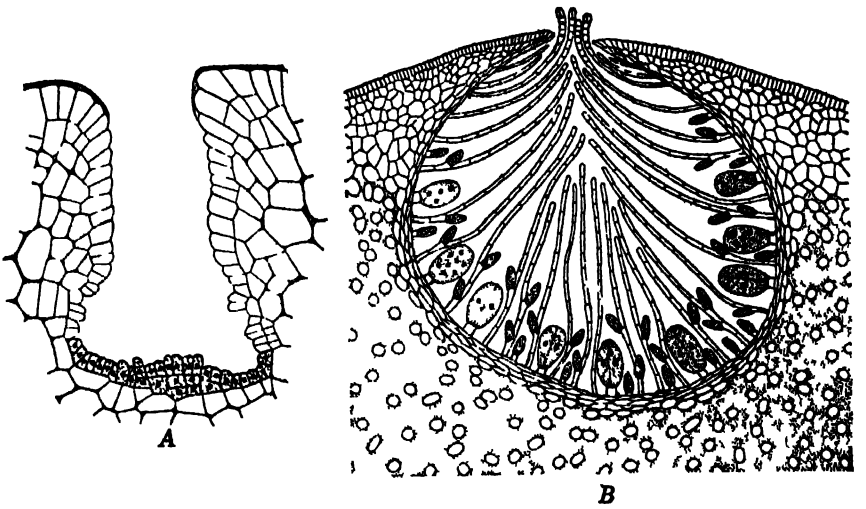


FIG 152.—*Pelvetia fastigiata* (J G Ag) DeToni *A* a young conceptacle after differentiation of fertile layer *B* diagrammatic transverse section of a thallus and vertical section of a mature conceptacle (*A*, × 215 *B* × 110)

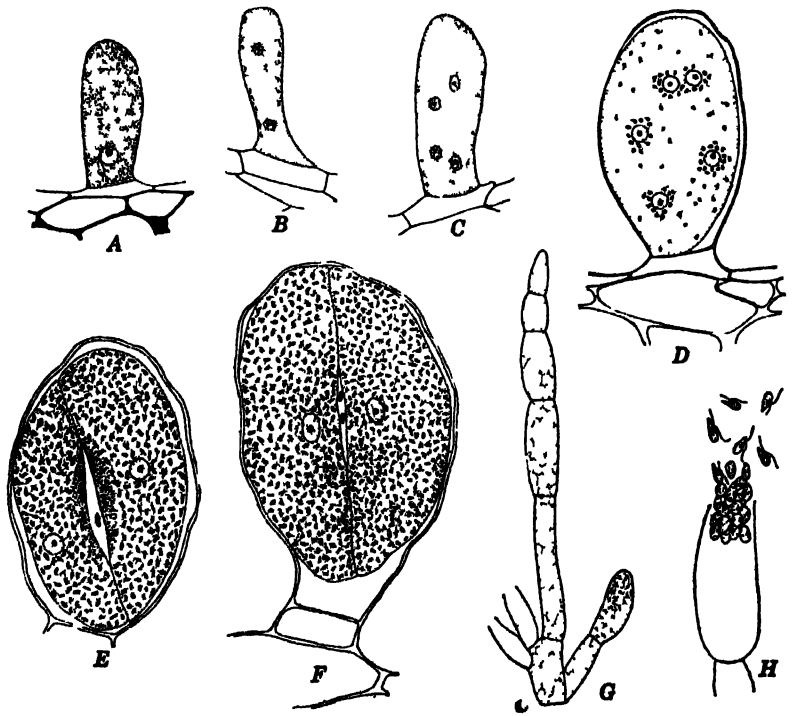


FIG 153.—*Pelvetia fastigiata* (J G Ag) DeToni *A–F*, stages in development of macrosporangia *G*, paraphysis bearing microsporangia *H*, liberation of microspores. (*A–G*, × 325, *H*, × 650)

versely into a stalk cell and a macrosporangial cell, neither of which divides again (Fig. 153*A*). The macrosporangial cell increases greatly in size and becomes the macrosporangium Eight nuclei are formed by three successive divisions, and it is very probable that the first two are reductional (Fig. 153*B–D*). The eight-nucleate protoplast then cleaves into two aplanospores (eggs), each generally with four nuclei (Fig. 153*E–F*). This cleavage is vertical in *P. fastigiata* and transverse in *P. canaliculatus* (L.) Dec'ne and Thur. One nucleus of each aplanospore enlarges and becomes centrally located, the remaining nuclei move to the recently formed plasma membrane and become cut off.[1] Cleavage is irregular in about 10 per cent of the macrosporangia of *P. fastigiata* and produces three to six aplanospores

The macrosporangial wall becomes differentiated into two relatively firm layers, the *exochite* and the *mesochite*,[2] separated from each other by a softer gelatinous layer,[3] the *mesogelatin* (Fig. 151*A*, *G*). A portion of the wall between sporangium and stalk remains homogeneous and constitutes the *basal pit* of the wall

Liberation of zoospores (antherozoids) and aplanospores (eggs) takes place when *Pelvetia* is reflooded by the incoming tide. The mesogelatin of a mature macrosporangium within a conceptacle imbibes water, swells, and ruptures the surrounding exochite The mesochite with its contained aplanospores is then pushed toward and out through the ostiole. This passive extrusion of macrosporangia seems to be due to a swelling of gelatinous material within the conceptacle During the first 10 minutes after extrusion, the two aplanospores within the mesochite begin to separate from each other and become irregular in outline (Fig. 154*B*, *C*). This is due to the swelling of a gelatinous layer, the *endogelatin*, internal to the mesochite The mesochite continues to swell for the next 20 minutes, and the aplanospores within it gradually become spherical (Fig. 154*D–E*).

Reflooding of the thallus also causes a rupture of the outer wall layer of mature microsporangia and an extrusion of the sporangial contents through the ostiole. The mass of zoospores is surrounded by a gelatinous envelope when it is extruded, but this soon dissolves and the zoospores swim freely in all directions Zoospores swarming in the vicinity of liberated macrosporangia swim through the mesochite, swim about slowly within this envelope, and unite with the aplanospores (Fig. 154*E*). Several other Fucales are known[4] to have this gametic union of zoospore and aplanospore followed by a union of the two nuclei.

The zygote secretes a wall and begins to germinate within a day or two. There is usually a fertilization of both eggs within a mesochite,

[1] Gardner, 1910; Moore, 1928 [2] Farmer and Williams, 1898
[3] Resuhr, 1935. [4] Farmer and Williams, 1898; Strasburger, 1897; Walker, 1931

but occasionally one remains unfertilized (Fig 154*F*) The mesochite persists for several hours after extrusion but disappears before the zygote

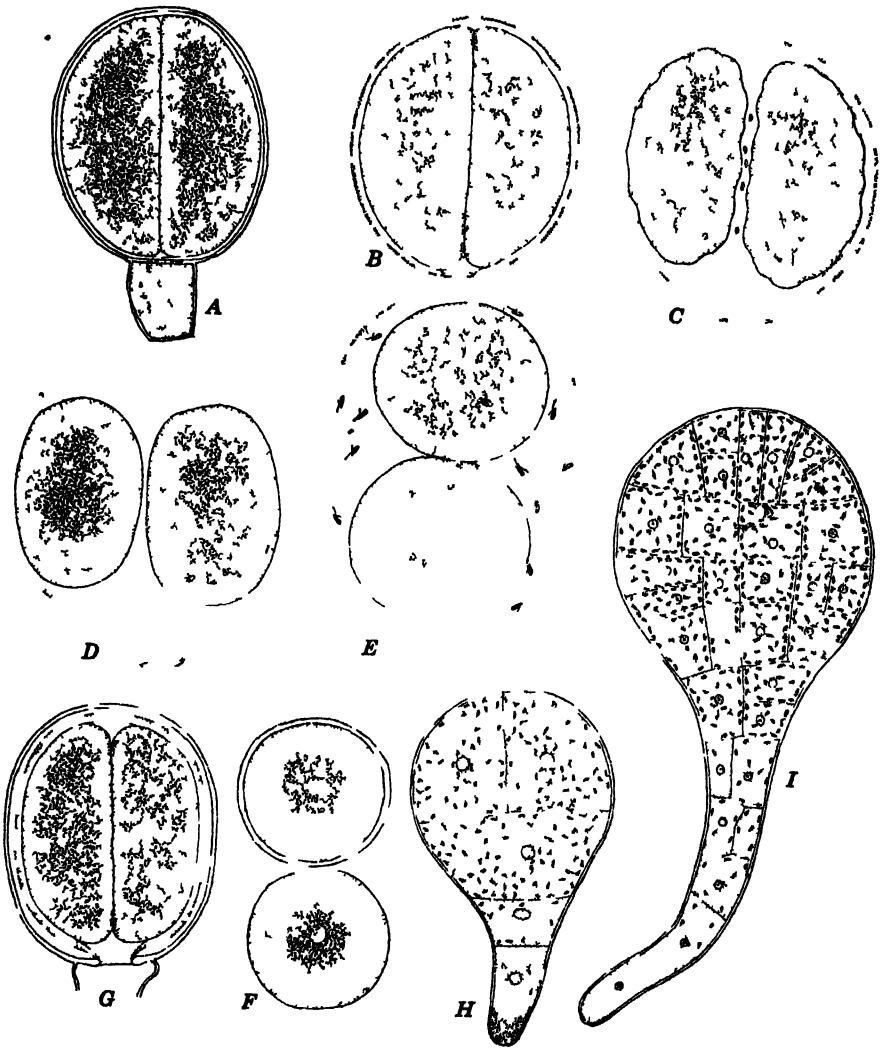


FIG 154 —*A–G Pelvetia fastigiata* (J G Ag) DeToni *A* mature macrosporangium *B–D*, stages in swelling of the mesochite and macrospores after their liberation from the ruptured exochite These three figures are the same sporangium drawn at 10 minute intervals *E* fertilization *F* a pair of macrospores several hours after liberation one fertilized the other unfertilized *G* macrosporangium soaked in sea water for several hours Compare with Fig *A* and note the abnormal swelling of the mesogelatin *H–I*, early stages in development of the thallus of *Hesperophycus Harveyanus* (Dec ne) Setchell and Gardner (*A–G*, × 215, *H I*, × 325)

divides Early stages in development of a zygote into a thallus are remarkably uniform from genus to genus among the Fucales. The nucleus may divide before the zygote has elongated, but in a majority

of cases the zygote is pear-shaped when the nucleus divides. The zygote divides transversely into an upper cell and a somewhat smaller basal cell. This is soon followed by a transverse division of the basal cell. The lowermost cell of a three-celled germling is a rhizoid initial; the upper end and median cells develop into the thallus proper.[1] The upper and median cells divide vertically, after which division is both horizontal and vertical (Fig. 154*H*). The rhizoidal initial undergoes two or three transverse divisions and then the uppermost cells divide vertically. Early development of a young sporophyte is at a rapid rate, and within five days it consists of 50 to 75 cells (Fig. 154*I*). Later development is much slower and gradually produces a short, erect, cylindrical thallus with several rhizoids at the lower end. Certain cells at the apex of the cylinder divide periclinally and develop into unbranched multicellular hairs. In germlings of *Fucus* these hairs begin to degenerate progressively toward the basal cell after they have attained a certain length.[2] The basal cell of one of the hairs then begins to function as an apical cell. All further growth of the sporophyte is initiated by this apical cell.

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CHAPTER VII

CYANOPHYTA

The Cyanophyta differ from all other algae in that their pigments are not localized in definite chromatophores but are distributed throughout the entire peripheral portion of a protoplast. The protoplasts contain a blue pigment (*phycocyanin*) in addition to chlorophyll and the accompanying carotinoids. They may also contain a red pigment resembling the *phycoerythrin* of Rhodophyceae. Another feature distinguishing Cyanophyta from other algae is the presence of a primitive type of nucleus (the *central body*) which lacks a nuclear membrane and nucleoli. Equally important, although negative in character, are the lack of flagellated reproductive bodies and the total lack of gametic union in all members of the division.

There are about 150 genera and 1,400 species, a majority of which are fresh-water.

The division contains but one class, the *Myxophyceae* (*Cyanophyceae*).

Occurrence. A large majority of the species in two of the three orders are fresh-water. The reverse condition obtains in the third order (Chamaesiphonales). Most marine species grow in the intertidal zone. Some of them are free-living; many more grow epiphytically upon other marine algae or within their tissues.

Fresh-water Myxophyceae are found in a wide variety of habitats. Many of them are aquatics that grow either in permanent or in temporary waters. Certain of those in permanent waters are found only in the plankton. They are usually present in abundance only during the warm months of the year. At such times one or two species may develop to such an extent that the water is colored by them. Such "water blooms" may be of sporadic occurrence, or they may occur annually.

Other fresh-water species are subaerial and grow either upon damp cliffs, dripping rocky ledges, or upon damp soil. Growths of terrestrial Myxophyceae are not usually conspicuous, but in certain regions, especially those with a pronounced rainy season, they may develop to such an extent that they form an extensive coating on the soil. Terrestrial Myxophyceae may also grow beneath the surface of the soil and at a depth of a meter or more.

Blue-green algae growing within, and in the outflow from, hot springs have long aroused the botanist's interest and have been studied in

practically every country where there are hot springs. Thermal algae may grow and multiply where the temperature is as high as 75°C. The frequently cited report[2] of Myxophyceae growing in hot springs with a temperature of 97°C. is undoubtedly incorrect. In fact, all records for the upper temperature limits at which thermal algae can exist must be scrutinized with care since portions of a spring but a few centimeters apart may differ in temperature by as much as 10°C. There are only a

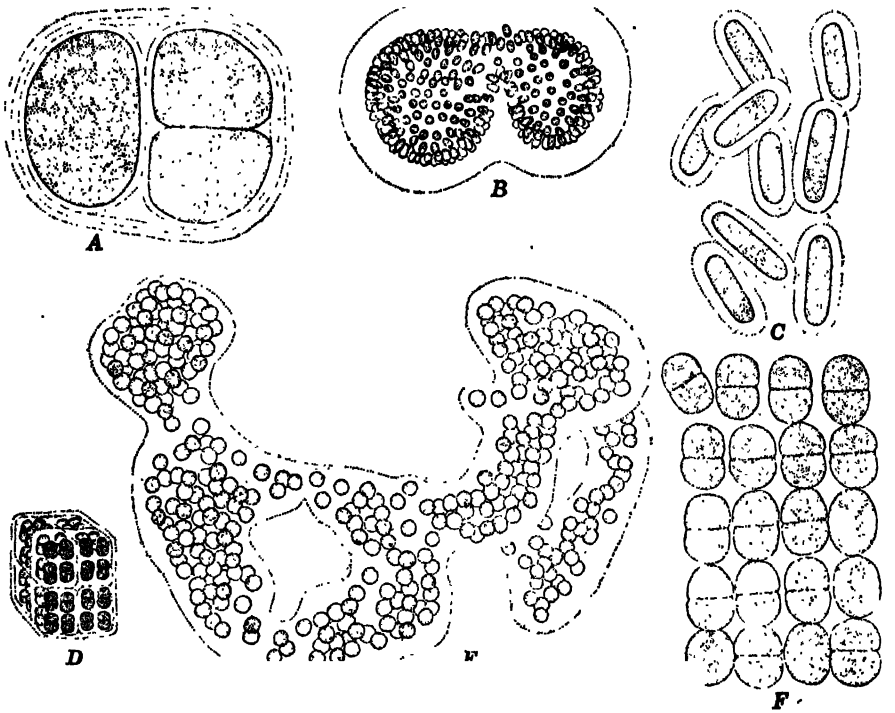


FIG. 155.—Nonfilamentous Myxophyceae. *A*, *Chroococcus turgidus* Näg. *B*, *Coelosphaerium Naegelianum* Unger. *C*, *Gloeothece linearis* Näg. *D*, *Eucapsis alpina* Clements and Shantz. (*After Clements and Shantz*, 1909.) *E*, *Microcystis aeruginosa* Kütz. *F*, *Merismopedia elegans* A. Br. (*A*, × 825; *B*, *E*, × 400; *C*, *F*, × 1,000; *D*, × 250.)

few species of thermal Myxophyceae, but they are world wide in distribution and are not found elsewhere than in hot springs and in their outflow.

Organization of the Thallus. A few Cyanophyta have an immediate separation of daughter cells after cell division and are therefore truly unicellular. In the great majority of species the daughter cells remain united after division, and this adhesion results in either a filamentous or a nonfilamentous colony.

[1] Setchell, 1903. [2] Brewer, 1866.

The production of nonfilamentous colonies (Fig. 155) results from a persistence and confluence of the gelatinous envelopes surrounding the individual cells. The confluence may be so complete that all traces of the individual sheaths disappear, or it may be incomplete so that there is a more or less evident sheath about each cell. Broadly speaking, genera with evident sheaths about the individual cells show a strong tendency toward colonial dissociation and have smaller colonies than do genera in which the cell sheaths are fused to form a homogeneous gelatinous matrix. The shape of nonfilamentous colonies is dependent upon the planes in which the cells divide. If divisions are in two planes, the result is a layer one cell in thickness and either a flat plate or a hollow sphere (Fig. 155*B*, *F*). When divisions are in three planes, their sequence may be so regular that there is a formation of a cubical colony (Fig. 155*D*), but the sequence of division is usually so irregular that there is no regular arrangement of the cells within a colony (Fig. 155*E*).

Repeated division in a single plane produces a filamentous colony (Fig. 156). Cells of filamentous colonies may be held together solely by walls common to two abutting cells, but usually there is also a cylindrical sheath of gelatinous material enveloping the file of cells. A single row of cells in a filamentous colony is called a *trichome*, and the trichome with its enclosing sheath is called a *filament*. According to the genus, a filament contains a single trichome (Fig. 156*F*), or it contains several trichomes (Fig. 156*G*). A trichome may be of the same diameter throughout, or it may be markedly attenuated at the distal end (Fig. 156*H*). Trichomes of most genera are unbranched, but there are also a few genera in which they are branched (Fig. 156*C*). Some genera with more than one trichome in a filament have them so arranged that they appear to be branched (Fig. 156*D*). This "false branching" is due to a growth of free ends of trichomes through the surrounding sheath.

The Cell Wall. Walls surrounding protoplasts of nonfilamentous Myxophyceae are composed of two concentric portions; a thin firm layer immediately outside of the protoplast and an outer gelatinous layer, the sheath, that is often of considerable thickness. The wall structure of filamentous blue-green algae is much the same, except that the gelatinous layer is restricted to free faces of the cells. For a number of years there was a very general acceptance of the investigations[1] which held that the thin inner portion of a wall is composed largely of chitin. More recent investigations are practically unanimous in denying the presence of chitin. Most of the recent workers[2] hold that cellulose is the chief chemical compound in this wall layer, but it has also been suggested[3] that

[1] Hegler, 1901; Kohl, 1903.

[2] Klein, 1915; Mameli, 1920; Panini, 1924; von Wettstein, 1921.

[3] Ullrich, 1929.

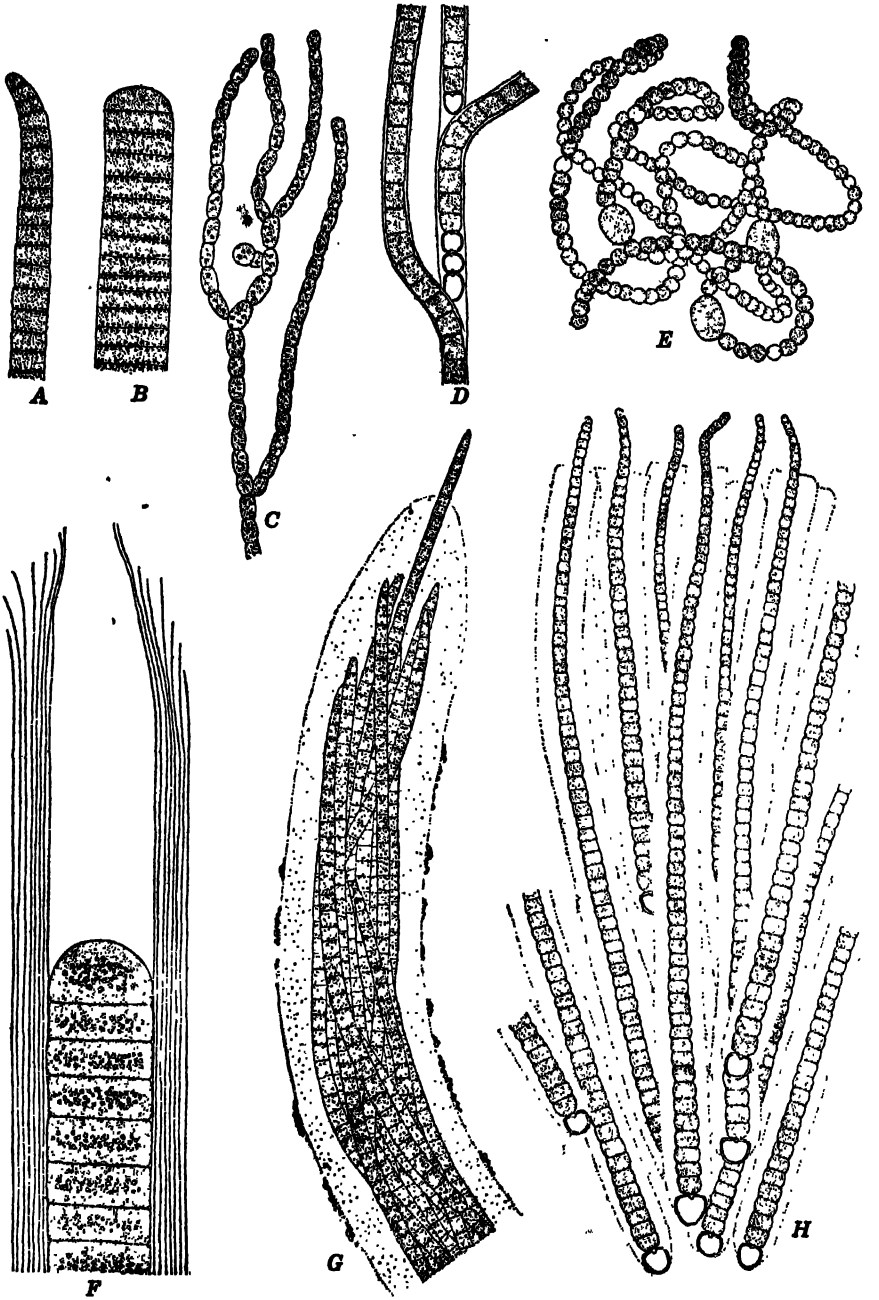


FIG. 156.—Filamentous Myxophyceae. *A*, *Oscillatoria formosa* Bory. *B*, *O. limosa* Ag. *C*, *Nostochopsis lobatus* Wood. *D*, *Tolypothrix tenuis* Kütz. *E*, *Anabaena circinalis* (Kütz.) Rab. *F*, *Porphyrosiphon Notarisii* (Menegh.) Kütz. *G*, *Microcoleus vaginatus* (Vauch.) Gom. *H*, *Rivularia dura* Roth. (*A–C*, × 650; *D*, × 375; *E*, × 400; *F*, × 600; *G*, × 300, *H*, × 485.)

it consists of a pectin-like hemicellulose. Recent investigators are also in accord in holding that pectic compounds are the predominant substances in the gelatinous portion of the wall.

The sheath surrounding a cell, or that surrounding a trichome, may be firm and conspicuous, or it may be of so watery a consistency and so inconspicuous that it is not visible unless demonstrated by special methods. The stratification evident in sheaths of many species (Fig. 156*F*) is probably due to a hydrolysis to different degrees of various portions of the sheath. Sheaths of most species are colorless, but those of some species are yellowish or brownish. This coloration has been thought to be due to the presence of special pigments, but there is no evidence at hand showing that sheath pigments are different from those found in the protoplast.

Many suggestions have been put forward concerning the function of the sheath, but none of them are applicable to all Myxophyceae. The presence of a sheath about a cell or a trichome undoubtedly increases the water-absorbing and water-retaining capacity and is one of the chief reasons why Myxophyceae are so successful in terrestrial and aerial habitats. The copious sheath generally found about colonies of most plankton species is also advantageous in that it makes the colony more buoyant. In most other aquatics it is not clear that the presence of a sheath is advantageous or disadvantageous.

Structure of the Protoplast. Ever since the first attempts[1] to determine the structure of the myxophycean cell there has been a recognition of the fact that its protoplast consists of a pigmented outer portion, sometimes called the *chromoplasm*, and an inner colorless portion, the central body. All investigations of cell structure by means of modern cytological technique find that all or a portion of the central body is differentially stainable in much the same fashion as is the chromatic material of true nuclei. The interpretation of these observations are, however, extremely divergent.

Some cytologists[2] maintain that the positive reaction of the central body to chromatic stains is not sufficient evidence for considering it nuclear in nature. The advocates of this interpretation think that the central body has the same fundamental structure as the peripheral portion of the protoplasm and that chromatic substances localized in the central portion of a cell, although aggregated in granules, have but little in common with true nuclear material (Fig. 157*B*). This contention seems to be denied by the recent[3] isolation of radicles of nucleic acid from blue-green algae.

[1] Schmitz, 1879, 1880.

[2] Fischer, 1905; Haupt, 1923; Hollande, 1933; Prát, 1925; Zacharias, 1890, 1892.

[3] Mockeridge, 1927.

A large majority of those studying the cytology of Myxophyceae think that the central body is nuclear in nature, even though it lacks a definite membrane and nucleoli. There are those[1] who think that the chromatic nuclear material is localized at certain junction points in the fundamental protoplasmic reticulum. These junction points may be equidistant from one another, or they may be irregularly spaced. Other cytologists hold that the entire central body is nuclear in nature and that it consists of chromatic materials more or less regularly distributed throughout an achromatic groundwork (Fig 157*A*) Advocates of

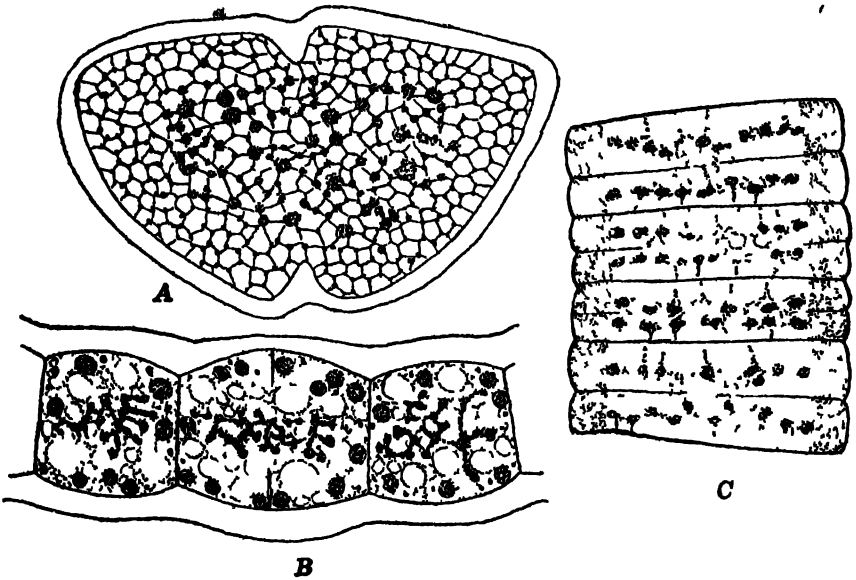


FIG. 157 —Cell structure of various Myxophyceae *A*, *Chroococcus turgidus* Nag *B*, structure and division of the cells of *Anabaena circinalis* (Kütz) Rab *C*, structure and division of the cells of *Oscillatoria princeps* Vauch (*A after Acton*, 1914, *B*, *after Haupt*, 1923, *C*, *after Olive*, 1904)

the interpretation that the central body is wholly nuclear in nature are not in agreement as to the method by which it divides Some of them[2] think that the mechanism dividing the primitively organized nucleus is a spindle apparatus resembling that of other plants (Fig 157*C*) It effects a division of the nuclear material by dividing the chromatin granules both qualitatively and quantitatively. One investigator[3] has even gone so far as to report definite chromosomes, but these observations have never been confirmed The remainder of those who think

[1] Acton, 1914, Guilliermond, 1906, 1925

[2] Baumgärtel, 1920, Brown, 1911, Lee, 1927; Olive, 1904; Phillips, 1904; Poljansky and Petruschewsky, 1929.

[3] Kohl, 1903

that the central body is nuclear in nature,[1] as well as all those who think that it is not nuclear, maintain that division of the chromatic material is amitotic and merely effects a quantitative bipartition of the chromatic substance.

The pigmented portion of a protoplast, the chromoplasm, is usually a fine alveolar reticulum. Included within it are a number of spherical or irregularly shaped inclusions. These may be irregularly distributed throughout the chromoplasm, or they may be restricted to the vicinity of walls abutting on other cells. It is clear that all of these bodies are not of the same chemical composition and that some of them, probably the majority, are reserve food materials. Evidence for this is seen both in their greater abundance in reproductive cells and in their gradual disappearance during periods of active growth or when plants are kept for some time in a dark room. The reserve food granules represent conversion products from sugars formed during photosynthesis, and, whatever else their nature, they are not starch. Many hold that glycogen is the chief food reserve accumulated within the myxophycean cell. Others[2] think that a true glycogen is never formed and that reserves accumulating in the chromoplasm are glycoproteins, using the term in the widest sense. In addition to glycogen or glycogen-like compounds, the chromoplasm may contain other reserve foods. These include granules that are wholly proteinaceous in nature, and also minute droplets of oil.

Differential staining of the central body[3] and microchemical studies[2] show that reserve foods may also accumulate in the central body. These seem to be of the same nature as those in the chromoplasm, and there seems to be but little support for the view[4] that a special carbohydrate (*anabaenin*) is formed in the central body.

There is a very marked diversity of opinion concerning the so-called *gas vacuoles* or *pseudovacuoles* found in many of the fresh-water plankton species (Fig. 158). At times all individuals of a given species in a plankton catch will contain pseudovacuoles; in other cases only certain of the individuals will contain them. In the latter cases the pseudovacuoles frequently appear in other cells a few hours after the collection is transported to the laboratory. When algae containing pseudovacuoles are viewed in a mass, it is of a pale yellowish-green color. When cells are seen under low magnification, the pseudovacuoles appear as black bodies, larger than other cell inclusions. They are scattered throughout the protoplast, and frequently they are present in such numbers that it is impossible to distinguish between central body and chromoplasm. Their reddish color, when examined under a high magnification, is probably

[1] Acton, 1914; Gardner, 1906; Guilliermond, 1906, 1925; Hegler, 1901.
[2] Baumgärtel, 1920. [3] Gardner, 1906. [4] Fischer, 1905.

a refraction phenomenon. The first studies,[1] which held them to be gas-filled cavities, were not particularly conclusive since they could not be repeated by others.[2] Recent investigations[3] seem to prove conclusively that pressure or a partial vacuum will cause the pseudovacuoles to disappear and gas bubbles to collect near the surface of cells. However, not all who have recently studied the problem think that these structures are gas-filled cavities, and the suggestion has been made[4] that they are cavities filled with a viscous substance. Among the functions ascribed to them have been that of giving plankton species a greater buoyancy and that of serving as a light screen against too intense illumination. It has also been suggested[5] that they do not serve any particular purpose but result from intramolecular respiration induced by an oxygen deficiency in the water.



FIG. 158.—*Anabaena circinalis* var *macrospora* (Wittr.) DeToni with pseudovacuoles in the vegetative cells and the akinete. (× 825.)

Pigments. Although some phycologists regard the pigmented portion of the protoplast as a single chromatophore, it is not a chromatophore in the same sense that the term is used in connection with other algae. In some cases the pigments appear to be uniformly diffused throughout the chromoplastic portion of the protoplast; in others the coloring matter appears to lie in minute granules scattered through the peripheral portion of the protoplasm.[6]

The pigments present in the chromoplasm include chlorophyll and the carotinoids usually associated with it, *phycocyanin*, and a red pigment similar to, but not identical with, the *phycoerythrin* of Rhodophyceae. So far as is known the chlorophyll and carotinoids are similar to those found in green plants. The phycocyanin[7] is a water-soluble substance which may be extracted by means of chloroform water and then precipitated in crystalline form by the addition of ammonium sulphate. If Myxophyceae are killed by the addition of a few drops of sulphuric acid or by suffocation through placing too much material in too small a container, the water surrounding them becomes a bright blue because of the water solubility of the phycocyanin. Phycocyanin is more stable in light than are the chlorophyll pigments, as is evidenced by the blue

[1] Klebahn, 1895, 1896, 1897. [2] Brand, 1901; Molisch, 1903.
[3] Klebahn, 1922, 1925. [4] Van Goor, 1925. [5] Canabaeus, 1929.
[6] Wager, 1903. [7] See Czapek, 1913 p. 598 for literature.

color of dried Myxophyceae that have been exposed to full sunlight for a few days.

Spectroscopic analyses of the red pigment in protoplasts of Myxophyceae seem to show that it differs slightly from the phycoerythrin of Rhodophyceae.[1] Because of this and because of differences in capillary analyses of red pigments in Rhodophyceae and Myxophyceae, the term *schizophycean phycoerythrin* has been proposed[2] for the red pigment of blue-green algae.

The various pigments found in the myxophycean cell are not present in equal amounts nor are all of them always present. Some blue-green algae lack schizophycean phycoerythrin; others lack or contain only small amounts of phycocyanin.[2] Variations in proportions of red, blue, and yellow pigments should, from the theoretical standpoint, make possible any color in the protoplasts of Myxophyceae. The occurrence of grass-green, blue-green, olive, yellow, orange, pink, red, violet, purple, brown, and black Myxophyceae shows how closely this theoretical condition is approximated in nature. However, it should be noted that all such shades and colors in an algal mass are not always due entirely to pigments in the chromoplasm but may be due partially to colors in the gelatinous sheaths.

The causes for development of the various pigments in different proportions are not known with certainty. The theory of *complementary chromatic adaptation* was first applied[3] to the Myxophyceae to explain experiments which showed that certain of them cultivated in light of different colors assumed different colors. This theory, originally evolved to explain variation in color of Rhodophyceae,[4] holds that the color of the light-assimilating portion of the protoplast is directly complementary to the quality (color) of the light in which the plant is growing. For example, plants growing in blue light are red, and those in red light are green. Such color changes, sometimes called *Gaidukov phenomenon*, have been found for a number of Myxophyceae,[5] but it has also been shown that many members of the class do not give this response. Thus, in one series of experiments,[6] only 4 of 18 species investigated gave a definite Gaidukov response. Spectroscopic analyses of the species exhibiting chromatic adaptation showed that alternations in color were due to changes in the ratio between phycocyanin and schizophycean phycoerythrin. The change in color of species showing the Gaidukov phenomenon may also be due to factors other than light. Chief among them is the exhaustion of nitrogen from the substratum.

[1] Boresch, 1921; Wille, 1923. [2] Boresch, 1921.
[3] Gaidukov, 1902, 1903. [4] Engelmann, 1883, 1884.
[5] Boresch, 1919, 1921*A*; Gaidukov, 1923; Harder, 1922; Susski, 1929.
[6] Boresch, 1921*A*.

Opponents[1] of the theory of complementary chromatic adaptation hold that nutrition effects are the sole cause for the color changes found in cultures of blue-green algae. The truth lies somewhere between the two extremes; and the color of Myxophyceae growing under natural conditions is a light response in certain cases only. The best natural example of the Gaidukov phenomenon is the universal red color of Myxophyceae when they grow several meters below the surface of a lake or other deep body of water.

Movements of Myxophyceae. Many of the filamentous species, especially of genera belonging to the Oscillatoriaceae, have the ability to move spontaneously. The movement may be a forward and backward gliding of the trichome, a spiral progression or retrogression, or a slow waving of the terminal portion of a trichome. Movements of Nostocaceae[2] are usually restricted to few-celled germlings or to short segments (hormogones) cut off from adult trichomes.

The rate of movement is markedly affected by external factors, chief among which are light and temperature Increased illumination is accompanied by an increase in the rate of movement; with increase of temperature from 0 to 30°C., there is a doubling of speed for each 10° the temperature increases.[3] The rate of movement is also correlated with the osmotic pressure and with the diameter of the cells.[4]

Movement of Myxophyceae has been ascribed to growth of the trichome, to osmotic currents, to the presence of cilia on the terminal cells, to peristaltic contractions, and to the secretion of gelatinous materials.[5] During the past 15 years most of those studying the problem have thought movement to be due either to gelatinous secretions or to peristaltic contractions. The theory that locomotion is due to a secretion of gelatinous material, although suggested quite early,[6] received but little serious consideration until it was definitely established that the slow locomotion of desmids is due to a slime mechanism (page 86). As applied to Myxophyceae, it is held[7] that forward progression is due to a rapid swelling of gelatinous material secreted through the cell walls. Some advocates of this theory think that the gelatinous material is secreted through minute pores in the wall and that rotating movements are due to an arrangement of the pores in two crossing-spiral series. The terminal cells of trichomes have been thought to be of major importance in locomotion by secretion, but it has been shown[8] that trichomes

[1] Magnus and Schlindler, 1912; Pringsheim, 1914; Schindler, 1913.
[2] Castle, 1926; Harder, 1918.
[3] Nienburg, 1916; Pieper, 1913; Schmid, 1918. [4] Burkholder, 1934.
[5] See West, 1916, for a review of the various theories. [6] Siebold, 1849.
[7] Fechner, 1915; Harder, 1918; Prell, 1921; Schmid, 1918, 1921, 1923.
[8] Schmid, 1923.

whose apical cells have been killed by reagents, as sulphuric acid, do not lose their ability to move spontaneously Not all recent workers on the problem have subscribed to the theory of locomotion through slime secretion, and movements of myxophycean trichomes have also been ascribed[1] to rhythmic waves of alternate expansions and contractions passing along the length of a trichome

Vegetative Reproduction. The only regular method of reproduction in all genera referred to the Chroococcales is that of cell division. Ordinarily, the two daughter cells remain united to each other within a common gelatinous envelope, and the indefinite repetition of cell division results in a nonfilamentous colony containing many cells. Colony

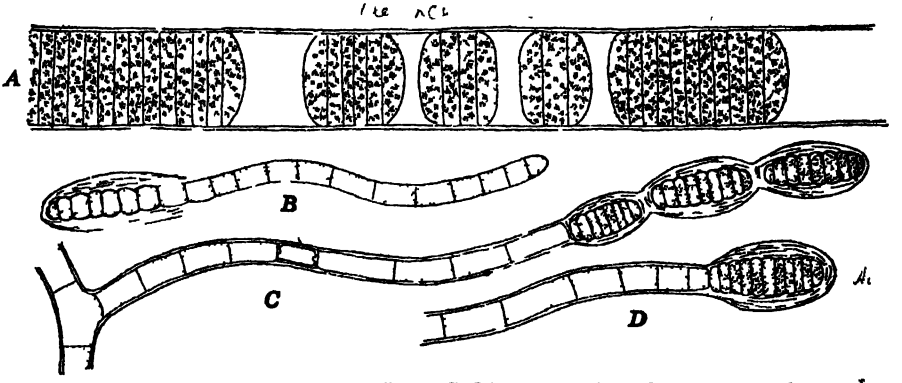


FIG 159 —*A*, hormogones of *Lyngbya Birgei* G M Smith *B–D* hormospores of *Westiella lanosa* Frémy (*B D after Frémy*, 1930) (*A* × 730, *B–D*, × 375)

reproduction is a matter of chance and depends upon an accidental breaking of the colonial envelope. If the envelope is soft and tends to dissolve, the colony never grows to a large size before it becomes separated into two or more portions. In genera with a tough envelope, the colony usually becomes many-celled before it breaks into smaller portions

Trichomes of filamentous genera are, from the theoretical standpoint, capable of indefinite growth in length, but under ordinary conditions they break into two or more portions before they attain any great length. Breaking may be due to animals biting through the middle of a filament, to the death of certain cells in the row, or to a weaker adhesion between certain cells than between others. Instances of the last sort are mostly among genera which produce heterocysts (page 290), and the zone of weak adhesion is where a heterocyst and a vegetative cell abut on each other.

Many filamentous genera regularly delimit short sections of trichomes, and these *hormogones* are an important method of propagation among

[1] Ullrich, 1926, 1929

filamentous Myxophyceae (Fig. 159*A*). Hormogones are delimited by a development of double concave disks of gelatinous material (*separation disks*) between two adjoining vegetative cells. The formation of hormogones and separation disks is seen to best advantage in large-celled species of filamentous genera with discoid or cylindrical cells. Here the hormogones may be but two or three cells in length, or they may be several cells long. Hormogones have an even greater capacity for locomotion than do vegetative trichomes, and, sooner or later after the hormogones are formed, they move away from the filament in which they were produced and grow into new filaments. Hormogones usually develop directly into typical filaments, but occasionally[1] the juvenile filament produced by a germinating hormogone has but little resemblance to an adult one.

Hormogones developed at the tips of trichomes of certain genera have differently shaped cells and much thicker walls (Fig. 159*B–D*). These multicellular spore-like bodies are *hormospores*.[2] They germinate directly into new filaments.

Spore Formation. Zoospores and flagellated gametes have never been observed among the Myxophyceae, and there is no reason for expecting that they will be discovered in the future. However, many of the blue-green algae are known to produce nonmotile spores.

Most of the filamentous genera, except those belonging to the Oscillatoriaceae, regularly have certain cells of a trichome developing into nonmotile spores. Development of these spores begins with an enlargement of, and an accumulation of food reserves within, a cell. During the later stages of spore development, there is an appreciable thickening of the wall, and this is often accompanied by a differentiation of distinct exospore and endospore wall layers. This type of spore, which contains the entire protoplast and in which the original wall of the vegetative cell is the outermost portion of the spore wall, is called an *akinete*. Cells developing into akinetes usually lie isolated from one another along a trichome, but in certain genera several successive cells may develop into akinetes (Fig. 160). An akinete may be formed at a specific place in a trichome, or it may develop anywhere along a trichome. If it develops in a specific place, it is always next to a heterocyst, either one at the end of a trichome or one that is intercalary in position.

Resting spores of the akinete type, which are structures for tiding the alga over unfavorable periods, usually germinate into a vegetative filament as soon as favorable conditions return. One of the best examples of this is seen in the regular germination of akinetes of several terrestrial species immediately after a heavy rain and a thorough soaking of the soil. Akinetes may retain their viability for extremely long periods, and it

[1] Geitler, 1921. [2] Borzi, 1914; Frémy, 1930; Geitler, 1930–1932.

has been shown[1] that there was a germination of them from samples of dried soil that had been stored for 70 years. However, akinetes are not absolutely necessary to tide Myxophyceae over long unfavorable periods since, in the experiments just cited, it was found that genera that do not form akinetes could withstand storage for 50 years.

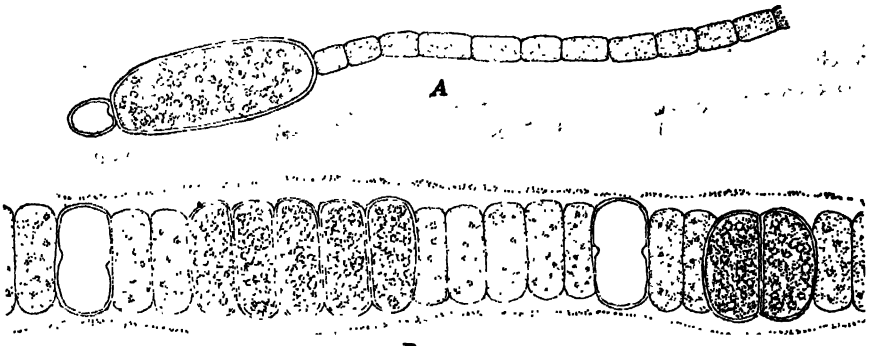


FIG. 160.—Akinetes. *A*, *Cylindrospermum muscicola* Kütz. *B*, *Nodularia spumigena* Mertens. (× 900.)

A germinating akinete (Fig. 161) usually grows directly into a more or less typical filament, but there may be a formation of a juvenile structure with but little resemblance to the mature trichome.[2] In most cases germination begins with a transverse division of the protoplast, and there may be several additional transverse divisions before it grows through the end of the softened or ruptured spore wall.[3] Less frequently, germination begins with a gelatinization of the inner spore-wall layer and a bursting of the outer layer. The undivided protoplast may be extruded after these changes in the spore wall, or it may divide transversely before it is extruded. Germlings from akinetes of many species are frequently motile, and, up to the time they become several cells in length, they may glide backward and forward in and out of the old akinete wall.[4]

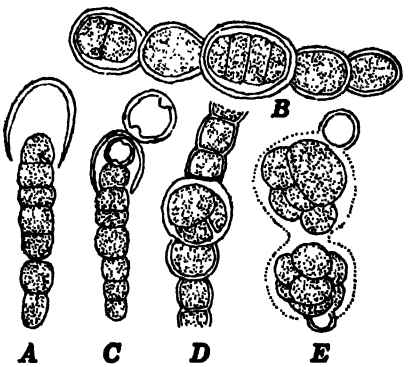


FIG. 161.—Germination of akinetes of Myxophyceae. *A*, *Anabaena oscillarioides* Bory. *B–C*, *A. sphaerica* Born. and Flah. *D–E*, *Nostoc muscorum* Küts. (*After Bristol*, 1920.) (× 825.)

All genera of the Charnaesiphonales and a few genera of other orders[5] have the protoplasts of all or of certain cells dividing to form a number of

[1] Bristol, 1919, 1920. [2] Bristol, 1920.
[3] Bristol, 1920; Fritsch, 1904; Rose, 1934; Spratt, 1911.
[4] Harder, 1918. [5] Brand, 1903; Schmidle, 1901.

small spores. These are usually called *endospores*, but they are similar to the aplanospores of Chlorophyceae in that the spore wall is not fused with the wall of the parent cell. In most cases there is a repeated division of the entire protoplast to form a mass of endospores that completely fill the old parent-cell wall, the sporangial wall (Fig. 162*A*). These endospores are usually spherical, but they may be angular because of mutual compression. A distinction is sometimes made between endospore formation through bipartition of the entire protoplast and that in *Chamaesiphon* where the spores are successively cut off at the distal end of a protoplast (Fig. 162*B*). Spores produced in the latter manner have

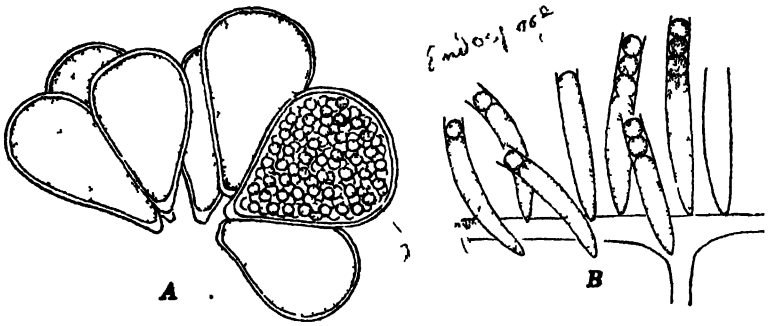


FIG 162.—Endospores. *A*, *Dermocarpa pacifica* Setchell and Gardner *B*, *Chamaesiphon incrustans* Grun (*A*, × 510 *B*, × 900)

been called *exospores*,[1] but such a distinction is needless because the exospore is only a special type of endospore.

Certain of the nonfilamentous Myxophyceae may have successive cell divisions following one another so closely that the daughter cells are very much smaller than ordinary vegetative cells. These *nannocytes*[1] look very much like endospores, but they are not true spores.

Heterocysts. All of the filamentous Myxophyceae but the Oscillatoriaceae regularly produce the special type of cell known as a *heterocyst*. They differ from vegetative cells and from spores both in structure of their walls and in their transparent contents. In most genera, heterocysts are developed isolated from one another in a trichome, but there are a few genera in which they regularly develop in adjoining pairs. Heterocysts of some genera are always terminal in position; those of other genera are intercalary (Fig. 156*E*, *H*).

Heterocysts arise by a metamorphosis of vegetative cells and usually only from recently divided ones. The metamorphosis may involve a change in shape, but in the majority of genera there is no appreciable change from the shape characteristic of a vegetative cell. The first step in heterocyst formation is a secretion of a new wall layer internal

[1] Geitler, 1925, 1930–1932.

to that originally surrounding the cell. Depending upon the terminal or intercalary position of the heterocyst in a trichome, there is a pore at one or at both poles of the new wall layer. Cytoplasmic connections with adjoining vegetative cells are usually evident through the polar pores, but, as the heterocyst approaches maturity, the pores become filled with prominent button-like thickenings of wall material, the *polar nodules*. The protoplast within a heterocyst becomes more and more transparent after the polar nodules have been formed. Preparations stained with iron-alum-haematoxylin show that transparency of a mature heterocyst is not due to a disappearance of the protoplast but to a transformation of it into a homogeneous viscous substance.

The nature and function of the heterocyst are topics that have been debated at length. Formerly there were quite diverse opinions concerning the nature of the heterocyst, but present-day opinion is more or less unanimous that it is spore-like in nature. The general agreement concerning its nature has come about through the accumulation of several well-authenticated exceptional cases[1] in which a heterocyst germinates to form a new filament (Fig. 163). The changes in nature and structure of the wall show that heterocysts are not analogous to akinetes. The non-akinete nature of the heterocyst is also shown by the formation and subsequent germination of endospores within a heterocyst.[2] These exceptional cases seem to show that heterocysts are reproductive structures, but structures which have become functionless as such, except in occasional instances.

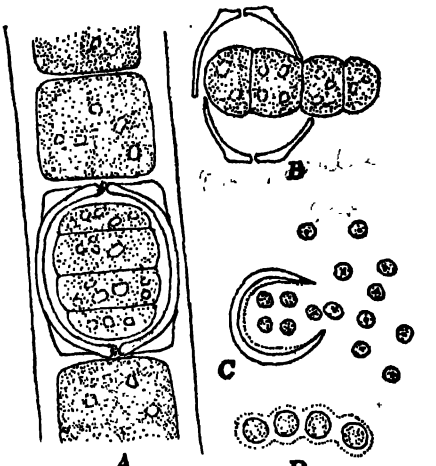


FIG. 163.—Germination of heterocysts of Myxophyceae. *A*, *Anabaena hallensis* (Janez.) Born. and Flah. *B*, *Nostoc commune* Vauch. *C-D*, *Anabaena Cycadeae* Reinke. (*A–B*, *after Geitler*, 1921; *C–D*, *after Spratt*, 1911.) (*A–B*, × 2,500; *C–D*, × 2,200.)

Although ordinarily functionless as spores, or sporangia, the heterocysts have in many instances taken on certain secondary functions. Sometimes they have a definite relationship to the development of akinetes, and certain genera always develop their akinetes next to a heterocyst. Heterocysts may also serve as a specific device for multiplication of trichomes; there are a number of species whose trichomes always fragment at the point where two heterocysts adjoin or at the juncture of a heterocyst and a vegetative cell. Genera with a true or a false branch-

[1] Brand, 1901, 1903; Canabaeus, 1929; Geitler, 1921. [2] Spratt, 1911.

ing may have a definite correlation between the position of a heterocyst and the point of origin of a true or a false branch.

Classification. Almost all systems for the classification of Myxophyceae divide them into three orders differing from one another in vegetative organization and in methods of reproduction. These three orders are:

Chroococcales in which the cells are either solitary or united in non-filamentous colonies. The only regular method of reproduction is that of vegetative cell division and fragmentation of colonies. The order includes about 35 genera and 250 species, almost all of which are fresh-water.

Chamaesiphonales in which the cells are generally epiphytic and either solitary, gregarious, or in colonies with a tendency toward a filamentous organization. The order is sharply differentiated from others of the class by the regular formation of endospores. There are about 30 genera and 130 species, most of which are marine.

Hormogonales in which the cells are united in definite trichomes that always have the capacity to form hormogones. Frequently, also, there is a formation of akinetes, of heterocysts, or of both. There are about 90 genera and 1,000 species, a large majority of which are fresh-water.

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CHAPTER VIII

RHODOPHYTA

The Rhodophyta, or red algae, are primarily distinguished from other algae by their sexual reproduction, in which nonflagellated male gametes are transported to, and lodged against, the female sex organ, the *carpogonium*. Some Rhodophyta have the zygote dividing directly into spores, but in most cases there is an indirect formation of spores from the zygote. The red algae also differ from all other algae except the Myxophyceae in their lack of flagellated asexual spores. Plastids of Rhodophyta contain a red pigment (*phycoerythrin*) in addition to chlorophyll. Sometimes there is also a blue pigment, *phycocyanin*. In the great majority of Rhodophyta, phycoerythrin is present in such quantities as to mask the other pigments and so give the plant a distinctive red color. However, color is not an absolute criterion in determining Rhodophyta, since many of the marine species inhabiting the upper littoral zone and most of the fresh-water species are green, olive-green, or golden brown.

All of the Rhodophyta are placed in a single class, the *Rhodophyceae*. This class contains some 400 genera and 2,500 species.[1]

Distribution. About 50 species, belonging to a dozen or more genera, are fresh-water in habit. Most of them are rather closely restricted to the well-aerated waters of rapids, falls, and mill dams in cold, rapidly flowing streams.

An overwhelming majority of the red algae are strictly marine. Under normal conditions all of the marine species are sessile, and in most cases death soon ensues if a thallus becomes detached and free-floating. Marine species are found in all oceans, including the Arctic and Antarctic, but only a small minority of the species grow in the polar seas. Geographical distribution of the marine species is generally correlated with the surface temperature of the ocean. The gradual increase in temperature of surface water as one passes from polar to tropical regions is correlated with a change in composition of the rhodophycean element in the flora. Most species of Rhodophyceae are confined to zones of amplitude of approximately 5°C. of the summer temperature, but certain species extend over zones representing 10°C. amplitude, and a few are

[1] Estimates of the number of Rhodophyta are based upon Schmitz and Hauptfleisch, 1896–1897; Svedelius, 1911.

known[1] in zones with an amplitude of 20°C. Thirty-four per cent of the marine species are found in extratropical waters of the northern hemisphere, 22 per cent are found in tropical waters, and 44 per cent in the imperfectly known extratropical waters of the southern hemisphere.[1]

There is also great variation in the vertical distribution of Rhodophyceae at any given station. Some species grow only in the intertidal zone, and even here there may be a distinct zonation. On the Monterey Peninsula, California, where the intertidal zone is about 2 meters in height, there are certain species restricted to the uppermost portion, others restricted to the middle portion, and still others restricted to areas exposed by the lowest tides only. Many of the species found low in the littoral belt also grow at levels never exposed by the tides. In most cases there is but little vertical zonation among the sublittoral red algae.[2] The maximum depth at which sublittoral algae will grow depends primarily upon the amount of light penetrating the water. This, in turn, depends upon the latitude and the turbidity of the water. Algae in the north Atlantic rarely grow below the 30-meter level.[3] Here the algae found at the lowest levels are almost exclusively Rhodophyceae. In Florida[4] and in the Mediterranean,[5] where the water is clearer and the sun more directly overhead, algae have been found in abundance at the 75- to 90-meter level. At these deepwater stations there are Chlorophyceae and Phaeophyceae intermingled with Rhodophyceae. The greatest depth at which algae have been found is about 200 meters.[6] They have been reported from much greater depths, but these records are considered extremely dubious.

A majority of the littoral marine Florideae grow upon rocks or upon some other inanimate substratum. There are also many species which grow upon other algae (Rhodophyceae, Phaeophyceae, or Chlorophyceae); most of them are restricted to a single host. The relationship may be one of epiphytism, internal space parasitism, or true parasitism. The truly parasitic species show more or less reduction in the amount of photosynthetic pigments, and there are certain colorless species which seem to obtain all of their food from the host.

Cell Structure. Cells of certain Rhodophyceae lack a central vacuole, but those of a majority of species have a large central vacuole and the cytoplasm restricted to a thin peripheral layer next the cell wall. The cell wall contains cellulose and various pectic compounds. In the subclass Florideae there is a pore-like opening in the wall between sister cells and a relatively broad cytoplasmic strand connecting the two protoplasts. Cells of vegetative branches, in a great majority of species, are uninucleate

[1] Setchell, 1915. [2] Børgesen, 1905.
[3] Børgesen, 1905; Hoyt, 1920; Printz, 1926. [4] Taylor, 1928.
[5] Funk, 1927. [6] Printz, 1926.

at all times; but vegetative cells of certain species are multinucleate and sometimes[1] have 3,000 to 4,000 in the larger cells. Resting nuclei are generally small, and often the only structures discernible are a sharply defined nuclear membrane and a large nucleolus separated from each other by an intervening hyaline area.

Cells of the more primitive Rhodophyceae generally have a single, centrally located, stellate chromatophore. At the center of this chromatophore is a dense, colorless, proteinaceous body, the pyrenoid. These "naked" pyrenoids lack the encircling sheath of starch grains usually found around pyrenoids of Chlorophyceae. The more advanced Rhodophyceae generally have discform chromatophores and more than one in each cell Chromatophores of these cells lack pyrenoids.

Carbohydrate reserves of red algae are usually stored in the form of small grains that lie in the cytoplasm outside the chromatophores. When these grains are treated with iodine, they become a light brown or a wine red, instead of taking on the deep-blue color so characteristic of the iodine-starch reaction On this account the insoluble carbohydrate reserve of red algae has been called *floridean starch* It has been held[2] to be a compound intermediate between true starch and dextrin Partial proof of this is shown by the fact that diastase obtained from red algae digests true starch very slowly[3] but digests dextrin more rapidly [4] Many red algae also accumulate a soluble sugar, *floridoside*,[5] it is a galactoside of glycerol

Pigments. Chromatophores of Rhodophyceae contain chlorophyll, but the component ratio differs from that in green plants [6] In addition to chlorophyll there is a water-soluble red pigment, phycoerythrin The presence of a blue pigment, resembling the phycocyanin of Myxophyceae, has been demonstrated[7] for a wide range of species, and it may possibly be present in all of them Variation in the proportions of chlorophyll, phycoerythrin, and phycocyanin accounts for the diversity of shades and color among the Rhodophyceae Intense illumination seems to favor the formation of phycocyanin and retard that of phycoerythrin. Because of this, most fresh-water species and marine species of the littoral zone rarely have the red color characteristic of Rhodophyceae. Marine species of the lower littoral and the sublittoral zones are generally a bright red or pink. Analyses of the amount of pigments in sublittoral species show[8] that the red color is due to a diminution in the amount of chlorophyll rather than to an increase in the amount of phycoerythrin.

[1] Lewis, 1909 [2] Bartholomew, 1914; Kylin, 1913
[3] Bartholomew, 1914. [4] Davis, A R , 1915
[5] Colin and Augier, 1933; Colin and Guéguen, 1930, 1933; Hass, Hill, and Karstens, 1935
[6] Boresch, 1932. [7] Kylin, 1912, 1931. [8] Lubimenko, 1926.

The function of the phycocyanin is unknown, and that of the phycoerythrin is a matter of dispute. According to the theory of *complementary chromatic adaptation*,[1] phycoerythrin is a photosynthetic pigment that functions in blue light. This theory holds that practically all of the photosynthetic activity in sublittoral Rhodophyceae is effected through the phycoerythrin, because these algae are growing in an environment where there has been a screening out of all but the blue light. Proof of the theory has been sought in comparative studies on the rates of photosynthesis when Rhodophyceae, Chlorophyceae, and Phaeophyceae are each exposed to red, green, and blue lights.[2] When the green alga *Enteromorpha compressa* (L.) Grev and the red alga *Delesseria sanguinea* (L.) Lamour. are exposed to weak light of different wave lengths, but of equal intensity,[3] the *Entermorpha* exhibits a higher rate of photosynthesis in red than in blue or green light, and the *Delesseria* shows but little difference in the three lights. The rate of photosynthesis has also been studied when Rhodophyceae, Phaeophyceae, and Chlorophyceae are lowered to various depths below the surface of the ocean Data obtained from such experiments[4] also seem to show that photosynthesis of Rhodophyceae is relatively more active 10 to 20 meters below the surface than is that of Chlorophyceae and Phaeophyceae. Practically all of those who have studied the phycoerythrin problem think that the ability of deepwater Rhodophyceae to carry on photosynthesis is in some way connected with the presence of phycoerythrin. Such a belief does not explain why certain Chlorophyceae and Phaeophyceae also function at deep levels. Photosynthesis has been shown[5] to be at the maximum when certain deepwater Rhodophyceae are submerged to a depth of 15 to 20 meters. This indicates that these deepwater red algae are comparable to shade-loving land plants and that, like them, they do not grow as well in more brightly illuminated habitats.

The Thallus. Except for two genera, all of the Rhodophyceae are multicellular. Some of the multicellular genera have the cells united end to end in simple or branching filaments. Others have a more complex plant body of definite macroscopic form and one that may be radially symmetrical or markedly compressed. Marine Rhodophyceae growing along the Atlantic Coast of the United States generally have small thalli that rarely attain a height of more than 10 cm. Marine Rhodophyceae on the Pacific Coast of this country tend to be somewhat larger, but only a few of them have thalli growing to a height of more than a meter.

Reproduction. Red algae seldom reproduce vegetatively by a fragmentation of the thallus. All of the Rhodophyceae form one or more

[1] Engelmann, 1883, 1884
[2] Ehrke, 1932; Klugh, 1930; Montefort, 1934.
[3] Ehrke, 1932.
[4] Ehrke, 1931; Gail, 1922; Montfort, 1934; Tschudy, 1934.
[5] Gail, 1922.

kinds of nonflagellated spores. *Carpospores*, found only in Rhodophyceae, are formed directly or indirectly from the zygote. All other types of spore are asexual in nature. These include *neutral spores*, *monospores*, *paraspores*, and *tetraspores*. Neutral spores are not formed in sporangia, and they may be produced by direct metamorphosis of a vegetative cell (*Asterocystis*, page 301) or by direct metamorphosis of daughter cells formed by repeated division of a vegetative cell (*Porphyra*, page 303). Monospores are always formed singly within sporangia borne upon the sexual generation (*Scinaia*, page 323). Sometimes the sporangium may become detached and float away from the plant producing it, but more frequently there is a rupture of the sporangial wall and an escape of the naked spore. Tetraspores are produced within sporangia borne upon diploid plants, and spore formation is preceded by a meiotic division of the single nucleus within the young sporangium; in practically all genera the protoplast of a tetrasporangium divides into four tetraspores. Paraspores are produced in considerable numbers within a sporangium borne upon a diploid plant, and they appear to be diploid.

Sexual reproduction of the Rhodophyceae is unlike that of any other algae, and a special terminology is applied to the structures involved in, and resulting from, sexual reproduction. The male sex organ of a red alga is a *spermatangium* (also called an *antheridium*), and it contains a single nonflagellated male gamete, the *spermatium*. The female sex organ, the *carpogonium*, is one-celled, and its distal end is prolonged into an outgrowth, the *trichogyne*. Spermatia liberated from spermatangia may be carried to, and lodge against, the trichogyne. Fertilization is effected by an entrance of the spermatium into the trichogyne and a downward migration of the spermatial nucleus to the female nucleus at the carpogonial base. In one subclass of red algae, the Bangioideae, there is a direct division of the zygote into carpospores. It is very probable that division of the zygote nucleus in Bangioideae is reductional. In the other subclass, the Florideae, the carpospores are formed indirectly from the zygote (page 309).

Relationships. Rhodophyceae, similar to the Chlorophyceae, are known with certainty from as far back as the Ordovician.[1] They must have arisen long before this because the oldest known fossils are related to advanced members of the class. However, the hypothesis[2] that Rhodophyceae are older than all other algae but Myxophyceae is based upon purely speculative assumptions.

The red algae differ so markedly in their nonflagellated reproductive cell and in the structures developed from the zygote that they appear to have arisen independently from other algae. All attempts to connect Rhodophyceae with other algae have centered around the Bangiales,

[1] Pia, 1927. [2] Tilden, 1935.

since this order is universally recognized as the most primitive among the red algae. Only two of the suggestions put forward merit serious consideration.

The stellate chloroplasts, thallus structure, and method of spore formation in *Prasiola* and *Porphyra* are strikingly alike.[1] Because of this, it has been held that the Bangiales have come from the Chlorophyceae via *Prasiola*, but the recent demonstration[2] that pigments of Bangiales and *Prasiola* are different indicates that the two are not related.

Myxophyceae and Bangiales are alike in that both have phycoerythrin and phycocyanin, both have a primitive type of nuclear division, and both lack flagellated reproductive cells. This has led to the suggestion[3] that the Bangiales originated among the Myxophyceae. However, an evolution of Bangiales from the Myxophyceae would involve the introduction of too many new features to make such an origin appear plausible. These features include: sexual reproduction, the presence of a definite chromatophore and pyrenoid, and a formation of a starch-like carbohydrate reserve.

Although there are but few botanists who think that the Rhodophyceae are related to other algae, there are many who think that the ascomycetes have been derived from them. This question will be considered on a later page (page 422).

Classification. The Rhodophyceae are divided into the following two subclasses:

Bangioideae in which growth of a thallus is intercalary and in which there is a direct division of the zygote into carpospores.

Florideae in which growth of a thallus is strictly terminal and in which carpospores are formed indirectly from a zygote.

SUBCLASS 1. BANGIOIDEAE

Thalli of Bangioideae may be simple filaments, branched filaments, solid cylinders, or expanded sheets one or two cells in thickness. Growth of a thallus is by intercalary cell division. There is no evident cytoplasmic connection between cells of a thallus. In most genera each cell contains a single central stellate chromatophore, but in a few genera they contain numerous parietal disciform chromatophores.

Asexual reproduction may be by means of neutral spores or by means of monospores. Sexual reproduction, when present, is by a direct division of a vegetative cell into many spermatia, which may be carried to, and fuse with, a vegetative cell functioning as a carpogonium. The zygote thus formed divides directly into carpospores.

[1] Lagerheim, 1892; Setchell and Gardner, 1920.
[2] Kylin, 1930. [3] Ishikawa, 1921.

There is but one order, the *Bangiales*. It includes some 15 genera and 60 species. These are placed in three families differentiated from one another by the manner in which asexual spores are formed. Sexual reproduction has not been found in many of the genera, but their systematic position is unquestioned because of their intercalary growth and their lack of cytoplasmic connection between the cells.

Asterocytis, a rare fresh-water genus in this country,[1] is representative of the simpler Bangiales. Its cells are spherical to broadly ellipsoidal. Each cell contains a single, bright blue-green, stellate chromatophore with a single large pyrenoid at its center (Fig 164*B*) Each cell is surrounded by a broad gelatinous sheath, quite distinct from the colonial

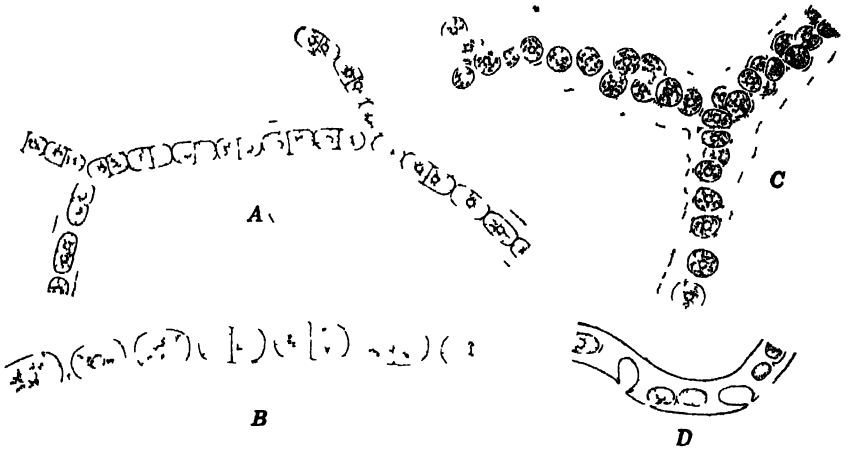


FIG. 164 — *A C*, *Asterocytis smaragdina* (Reinsch) Forti *A*, portion of a filament *B*, vegetative cells *C*, *Stigonema* like filament *D* filament of *A ramosa* (Thw.) Gobi after liberation of neutral spores (*D after Wille*, 1900) (*A*, *C*, × 325, *B*, × 650, *D*, × 240)

matrix. Division is intercalary and always at right angles to the long axis of a cell Now and then there is a change in orientation of an intercalary cell and a rapid division and redivision of it. This produces a lateral branch (Fig 164*A*). In certain colonies all the cells are rounded, and division takes place in all planes. This results in a palmelloid *Stigonema*-like or *Chroococcus*-like colony (Fig. 164*C*).

Asexual reproduction is by the direct functioning of the protoplast of a vegetative cell as a neutral spore. This spore is liberated[2] by a rupture of the surrounding gelatinous sheath (Fig. 164*D*). A liberated neutral spore secretes a wall and grows into a new filament after it has lodged on a suitable substratum. Thick-walled akinetes are also formed.[3]

[1] Smith, G. M , 1933 [2] Geitler, 1924; Wille, 1900.
[3] Kolderup-Rosenvinge, 1909–1924; Wille, 1900.

They are surrounded by a wall at the time they are liberated from the thallus producing them.

Porphyra, a marine genus with a dozen or more species, is a common alga along both the Atlantic and the Pacific coasts of this country. Most of the species grow attached to rocks in the littoral zone, but some species are epiphytic and restricted to a single host. For example, along the coast of California, *P. naiadum* Anderson grows only upon the marine angiosperm *Phyllospadix*, and *P. Nereocystis* Anderson grows only on stipes of one of the giant kelps [*Nereocystis Luetkeana* (Mert.) Post. and Rupr.]. The thallus of *Porphyra* is a smooth to greatly convoluted thin blade that is attached to the substratum by a disciform or a cushion-shaped holdfast (Fig. 165*A*). Blades of most species do not grow to a height of more than 20 to 50 cm., but those of certain species, as *P. Nereocystis*, may attain a height of more than 2 meters.

Europeans sometimes use *Porphyra* in making a soup. It is a highly esteemed foodstuff in the Orient, where it is used both in the making of soups and as a condiment. Most of the *Porphyra* used in the Orient comes from Japan, and in 1933 the market value of the year's crop[1] was slightly more than 10,000,000 yen ($5,000,000 at normal exchange). Some of the crop is sold fresh, but most of it is sun-dried before reaching the consumer. The supply is obtained almost exclusively from plants cultivated on suitable tidelands, and the annual return from a good "*Porphyra* farm" may run as high as $150 per acre.

The tidelands are prepared for cultivation by implanting numerous bundles of bamboo or brush in the muddy bottom of waters less than 3 to 5 meters deep. The bundles intercept and afford a lodgement for spores of *Porphyra* floating through the water. The bundles are set out about the first of October, and by the middle of November they are covered with germlings just visible to the naked eye. The plants attain full size in January, and the crop is then harvested.[2] Plants growing on the bundles begin reproducing early in the spring and disappear completely about the first of May.

The blade of a thallus is composed of cubical to broadly ellipsoidal cells. According to the species, they lie in a mono- or a distromatic layer within a homogeneous gelatinous matrix of a very tough consistency (Fig. 165*B*). Cell division may take place anywhere in the blade, but it is always in a plane perpendicular to the surface of the blade. When a blade is seen in surface view, the cells often lie in groups of two, three, or four, but there is little tendency toward a further grouping in squares as in *Prasiola*. *P. naiadum* has a cushion-like holdfast composed of parenchymatous cells.[3] All other species have a disciform holdfast

[1] Japan, Department of Finance, 1935.
[2] Smith, H. M., 1905; Yendo, 1919. [3] Hus, 1902.

composed of rhizoid-like outgrowths from cells in the lower portion of a blade. The rhizoids grow downward within the gelatinous matrix of a blade and then grow outward after reaching its base. Emergent portions of rhizoids are usually unbranched, unseptate, and with but little protoplasm. They grow in all directions and are densely intertwined with one another.



FIG. 165 – *Porphyra perforata* J. G. Ag. *A*, thallus. *B*, vertical section of vegetative portion of a thallus. *C*, *D*, vertical sections of thalli with carpogonia and developing carpospores. *E*, surface view showing liberation of carpospores. *F*, amoeboid carpospores. *G*, vertical section through portion of a thallus liberating spermatia. (*A*, × ½, *B–E*, *G*, × 325, *F*, × 650.)

Cells of *Porphyra* are without a central vacuole and contain a single large stellate chromatophore with a centrally located pyrenoid (Fig. 165*B*). Chromatophores of species growing high in the littoral zone may contain so much phycocyanin that the thallus is a deep olive-brown. The amount of phycocyanin in chromatophores of species growing in the lower littoral and sublittoral zones is generally so small that the color of the thallus ranges from pink to deep red. The single nucleus of the cell lies at one side of the chromatophore. In *P. tenera* Kjellm. it is a homogeneous body less than 2μ in diameter.[1] As this nucleus begins

[1] Ishikawa, 1921.

to divide a fusiform achromatic space appears at its center and this space increases in size as the nucleus becomes spindle-shaped. The peripheral material around the central space then splits into three longitudinal filaments. Each filament then breaks transversely into two daughter segments that move to opposite poles of the nucleus. Migration of the two daughter segments (chromosomes) to opposite sides of a cell is followed by a division of pyrenoid and chromatophore in a plane perpendicular to the thallus surface. The cell then divides in the same plane.

Conversion of vegetative cells into reproductive cells generally begins at the margin of a thallus. Sometimes, as in *P. perforata* J.Ag., vegetative cell division keeps pace with conversion into reproductive cells, and the thalli remain approximately constant in size throughout the entire growing season. In other species, as *P. tenera* Kjellm., there is but little vegetative division after reproduction begins; the thallus gradually decreases in size and eventually disappears.

The formation of asexual neutral spores is of rather rare occurrence in *Porphyra* and generally is found only in vegetative cells intermingled with carpogonia.[1] Division of vegetative cells into neutral spores may be distinguished from division of carpogonia into carpospores because the former is always in a plane perpendicular to the thallus surface.[2] Hence the neutral spores always lie in a monostromatic layer.

All species reproduce sexually. Fertile regions of a thallus are discernible to the naked eye because the spermatial masses are a much lighter color than vegetative cells and the masses of carpospores are darker. Some species are homothallic, others are heterothallic.

Sex organs of the homothallic *P. perforata* develop in patches at the margin of a thallus. A vegetative cell dividing to form spermatia undergoes successive vertical and transverse division until there are 128 colorless spermatia arranged in 8 tiers of 16 each.[1] The masses of spermatia formed from adjoining vegetative cells lie a short distance from one another within the gelatinous matrix of a thallus. Thalli exposed by the receding tide have more or less shrinking of the gelatinous matrix as it dries out during the intertidal exposure. When the plant is reflooded by an incoming tide, reswelling of the matrix squeezes the spermatial masses out to the thallus margin (Fig. 165*G*). This mechanical action may be compared to the squeezing of toothpaste from a tube. The fact that spermatia are extruded upon reflooding rather than during intertidal exposure may be demonstrated by comparing, under the microscope, dry and water mounts of material collected when the tide is out. The extruded male elements are so small that it is uncertain

[1] Hus, 1902. [2] Berthold, 1882.

whether they do or do not have a wall. They have been described as being naked[1] and as having a wall.[2] Thus it is uncertain whether they are spermatangia or spermatia. Whatever their precise nature, they are carried in all directions by water currents, and some of them are carried to, and lodge against, the trichogynes of carpogonia.

Carpogonia are formed by a slight metamorphosis of vegetative cells. A mature carpogonium is ellipsoidal and has a slight prominence at one or at both poles (Fig. 165*C*). The prominence is the trichogyne, and it generally extends to the surface of the gelatinous matrix of a thallus.[3] Union of spermatium and carpogonium may be gradual,[4] or there may be a sudden inflow of the spermatium into the carpogonium. Both spermatium and carpogonium have been shown[1] to be uninucleate at the time of union, but the actual fusion of male and female nuclei has not been observed. Fertilization is followed by vertical and transverse division of the zygote into a number of carpospores (Fig. 165*D*). Their number and arrangement is said to be constant for any species,[5] but this is doubtful. According to the species, 2 or 4, 4 or 8, 8 or 16, 16 or 32 carpospores are produced by division of the zygote. Each carpospore contains a single stellate chromatophore, somewhat darker in color than that of a vegetative cell. Discharge of carpospores of littoral species is similar to that of spermatia, and it takes place when thalli are resubmerged by the incoming tide (Fig. 165*E*).

The liberated carpospores are naked, and they move[6] about with an almost imperceptible amoeboid movement (Fig. 165*F*). Amoeboid movement continues for two or three days; then the carpospores become spherical, secrete a wall, and develop into protonema-like uniseriate filaments. Sooner or later the cells at the distal end of a filament divide longitudinally, and the cells at the proximal end put forth rhizoidal outgrowths.

SUBCLASS 2. FLORIDEAE

Thalli of Florideae always have more or less evident cytoplasmic connection between the cells, and in almost all cases growth is strictly terminal. Cells of the more primitive genera usually have a single stellate chromatophore; those of more advanced genera usually contain more than one parietal discoform chromatophore.

The carpogonia are borne terminally upon special branches (filaments), and there is always an indirect production of carpospores from the carpogonia. Carpospores are the only spores produced by certain

[1] Ishikawa, 1921; Joffé, 1896 [2] Grubb, 1924.
[3] Berthold, 1882; Grubb, 1924; Ishikawa, 1921; Joffé, 1896; Knox, 1926.
[4] Knox, 1926. [5] Hus, 1902. [6] Grubb, 1924; Kylin, 1921.

genera. Other genera produce one or more types of spore (monospores, polyspores, tetraspores, paraspores) in addition to carpospores.

The subclass contains some 375 genera and 2,500 species.

Vegetative Structure. All Florideae have a branched filamentous thallus. In some genera the various branches are free from one another; in other genera they lie more or less intermingled with one another within a common gelatinous matrix; in still other genera they are so closely applied to one another that the thallus seems to be parenchymatous.

Increase in number of cells is due to transverse division of apical cells at the tips of branches.[1] With the exception of a few anomalous genera,[2] there is no transverse division of the daughter cell cut off posterior to an apical cell. However, derivatives from an apical cell may increase to many times their original length and breadth. Apical organization of a plant body is according to one of two general types. In one case there is a *monoaxial*[3] or *central-filament*[4] type of organization, in which there is a single axial filament that gives off filaments laterally or on all sides. In the other case there is a *multiaxial* or *fountain type* of organization with a central core of axial filaments, each giving off lateral filaments.

Growth of the monoaxial type is initiated by transverse division of the apical cell. After a derivative has come to lie one, two, or more cells back from the apical initial, it sends forth a lateral outgrowth that soon becomes cut off as a lateral cell (Fig. 166*A*). This cell is the apical initial of a lateral filament, and it functions in precisely the same manner as the apical initial of the central axis. Cells back from the apical initial of a lateral filament may cut off initials of secondary filaments; this may continue until there are filaments of tertiary, quaternary, or higher orders. Every derivative cut off from an apical initial is connected to it by a strand of cytoplasm. Thus, by following the arrangement of cytoplasmic connections, one may recapitulate the sequence of development in branching thalli. The arrangement of the cytoplasmic connections in relatively young portions of "parenchymatous" thalli (Fig. 166*B*) shows that they are filamentous in nature and generally of a monoaxial type. This cannot always be determined with certainty in older portions of a thallus because there are secondary cytoplasmic connections which obscure the sequence of development.

Multiaxial thalli grow in the same manner as monoaxial ones, except that each filament in the axial core has an apical cell. Lateral filaments from an axial filament are developed only on the free face not in contact with other axial filaments. Therefore mature portions of such thalli have a central core of longitudinal filaments surrounded by an ensheathing layer of lateral filaments (Fig. 170*B*).

[1] Schmitz, 1883 [2] Kolderup-Rosenvinge, 1909–1924; Kylin, 1924, 1928.
[3] Smith, G. M., 1933 [4] Oltmanns, 1922.

Thalli of some Florideae are perennial. The entire thallus may persist throughout the year, or the major portion of it may disappear during winter and the persistent basal portion proliferate new outgrowths the next year. Other Florideae are annual, with all thalli developed from sporelings each growing season. An all-year-round survey of the algal flora of the Isle of Man[1] has shown that the number of perennials is considerably greater than that of the annuals. Most of the extratropical annuals develop and fruit during the summer. This tendency is not so marked in the perennials, and fruiting individuals of many species are present throughout the year. Florideae with free-living sexual and

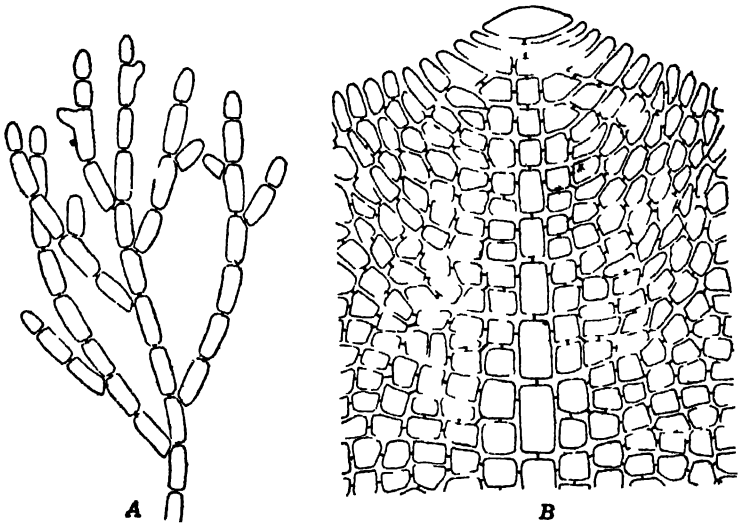


FIG. 166.—*A*, diagram of loosely branched monoaxial thallus of *Chantransia*. *B*, diagram of pseudoparenchymatous monoaxial thallus of *Grunelia*.

tetrasporic generations generally have the two fruiting at different seasons, but the periods of the two frequently overlap.

Reproductive Organs of the Gametophyte. The sexual plant (*gametophyte*) may produce sex organs only, or it may bear both sporangia and sex organs. In practically all cases asexual reproduction of the gametophyte is due to a production of *monospores* which are formed singly within *monosporangia* (Fig. 175*C*). Monosporangia of most species are emergent globose bodies quite different in shape from vegetative cells. The monospore within a monosporangium is discharged as a naked amoeboid protoplast[2] which eventually comes to rest, secretes a wall, and develops directly into a new plant. There are also gametophytes with sporangia containing more than one spore. These *polyspores* may be

[1] Knight and Parke, 1931. [2] Svedelius, 1917.

borne in distinctive sporangia or in sporangia indistinguishable from vegetative cells.[1]

Gametophytes of a majority of the Florideae are homothallic, but there are also many heterothallic species. The female sex organ, the carpogonium, is developed terminally, on a special laterally borne *carpogonial filament*. The *supporting cell*, the one producing the initial cell of a carpogonial filament, is differentiated close to the growing apex of a thallus. The supporting cells usually lie remote from one another, but they sometimes adjoin one another in a sorus-like group. Sorus-like fertile areas of Rhodophyceae, whether carpogonial, spermatangial, or sporangial, are called *nemathecia*. Most carpogonial nemathecia lie at the base of cavities (*conceptacles*) developed beneath the surface of a thallus (Fig. 181*B*). Carpogonial filaments are usually readily distinguishable from vegetative filaments because their cells lack chromatophores and have denser protoplasts. Carpogonial filaments of most genera are three or four cells in length and have no lateral branchlets, but there are certain genera (Fig. 180*A*) in which they are more than a dozen cells in length and have lateral branchlets from the lowermost cells. In the vast majority of species the carpogonium is the terminal cell of a carpogonial branch, but isolated cases have been reported[2] where the carpogonia are intercalary. Carpogonia of Florideae always have the distal end prolonged into a conspicuous *trichogyne* (Fig. 169*D*). Several genera have an obvious constriction where the trichogyne adjoins the carpogonial base. Because of this, it has been held[3] that originally the carpogonium was a two-celled structure. Carpogonia of most Florideae have a single nucleus, but a considerable number of species is known[4] in which there is also a nucleus in the trichogyne.

The male sex organ, the *spermatangium*, is developed terminally or subterminally upon a *spermatangial mother cell*. Sometimes the spermatangial mother cells are indistinguishable from vegetative cells, but more frequently they are the terminal members of branchlets in a two- to five-times-divided special filament. Filaments producing spermatangia may be borne singly upon the thallus or grouped together in nemathecia.

The spermatangial mother cell is always uninucleate and has the nucleus basal in position.[5] The first step in production of a spermatangium is a development of a protuberance at the distal end of the spermatangial mother cell. This is accompanied by a division of the nucleus and a migration of one of the daughter nuclei into the protuberance. There then follows a ring-like ingrowth of the lateral

[1] Howe, 1914. [2] Kolderup-Rosenvinge, 1909–1924. [3] Svedelius, 1917*A*.

[4] Grubb, 1923*A*; Kylin, 1914, 1916, 1916*A*; Svedelius, 1914, 1915, 1917, 1933; Yamanouchi, 1906, 1921.

[5] Grubb, 1925.

wall in the region where protuberance and mother cell adjoin.[1] The resultant uninucleate cell, the spermatangium, may be globose or elongate. Many species have the mother cell regularly budding off a second spermatangium; there are certain species in which a third and a fourth are formed.

The uninucleate protoplast (the *spermatium*) of a spermatangium is usually colorless, but there are a few species[2] in which it contains a chromatophore. Many species have been shown to have a rupture of the spermatangial wall and an escape of the spermatium. The liberated spermatium is always surrounded by a delicate wall,[1] but it is uncertain whether this is the innermost layer of the spermatangial wall or a structure entirely distinct from it. Certain species have been described[3] as having an abscission of the entire spermatangium, but this appears to be doubtful. Discharge of the spermatium may be followed by development of another spermatangium within the old spermatangial wall, and this may be repeated[4] until there are the remains of several spermatangial walls nested one inside another

Fertilization. Spermatia carried about by water currents may be transported to, and lodge against, trichogynes projecting beyond the thallus The sticky gelatinous sheath about the projecting portions of many trichogynes greatly increases the chances for adherence once a spermatium has lodged against it. Fertilization begins with a breaking down of spermatial and trichogynal walls at the point of mutual contact. The spermatial protoplast migrates into the trichogyne, after which the spermatial nucleus migrates down to the carpogonial base and there fuses with the carpogonial nucleus.[5] In a few species the spermatial nucleus divides[6] as it migrates down the trichogyne, and one of its daughter nuclei then fuses with the carpogonial nucleus.

Certain genera, all belonging to the Nemalionales, have been shown[7] to have an immediate reduction division of the zygote nucleus. In all other Florideae except the Nemalionales, the zygote nucleus divides equationally, and meiosis does not take place until after development of the free-living tetrasporic generation.[8]

Development of Carpospores. Gametic union, with or without an immediately succeeding meiosis, is followed by a development of *gonimoblast filaments*. Several species have also been thought to be parthenogenetic and to produce gonimoblast filaments without a preceding

[1] Grubb, 1925 [2] Cleland, 1919; Dunn, 1917; Osterhout, 1900.
[3] Dunn, 1917; Yamanouchi, 1906. [4] Cleland, 1919.
[5] Kylin, 1916; Lewis, 1909; Svedelius, 1914, 1915, 1933; Yamanouchi, 1906, 1921.
[6] Cleland, 1909; Kylin, 1916*B*, 1917.
[7] Cleland, 1919; Kylin, 1916*B*, 1917; Svedelius, 1915, 1933.
[8] Kylin, 1914, 1916; Lewis, 1909; Svedelius, 1914, 1914*A*; Westbrook, 1928; Yamanouchi, 1906, 1921.

gametic union. These presumed cases of parthenogenesis are extremely dubious, because the presumption is merely based upon a failure to find plants with spermatangia. The possibility of parthenogenesis among Florideae cannot be denied completely because one species has been shown to have a diploid gametophyte.[1] Although this species produces tetraploid gonimoblasts after a union of two diploid gametes, there is also a possibility that it produces a diploid gonimoblast and carpospores without any gametic union.

Some Florideae have the zygote nucleus, or its haploid daughter nuclei, remaining in the carpogonium, and the gonimoblast filaments growing directly from the carpogonial base (Fig 171*C–D*). Other Florideae have the zygote nucleus migrating from the carpogonium into another cell of the thallus and an outgrowth of gonimoblast filaments from this *auxiliary cell.* In some genera the supporting cell of the carpogonial filament functions as the auxiliary cell (Fig 184*B*). In other genera the auxiliary cell is a member of a one- or two-celled filament arising from the supporting cell of the carpogonial filament (Fig. 188*B*) In still other genera the auxiliary cell is an intercalary cell of a special filament arising remote from the carpogonial filament (Fig 179*B*) There are also many genera in which the auxiliary cell is an intercalary vegetative cell of the thallus, and one adjacent to or remote from the carpogonial filament (Fig 185*C*) Establishment of connection between carpogonium and auxiliary cell is due to the development of a tubular outgrowth, the *ooblast*, from the carpogonial base This is very short where carpogonium and auxiliary cell adjoin each other, but it is quite long when the two are remote The carpogonium or cells of the gonimoblast filaments may establish a vegetative connection with other cells of the thallus. These cells have been called *nurse cells*[2] because they are primarily nutritive in nature. Nurse cells may be solitary or may adjoin one another to form a *nurse tissue*

Gonimoblast filaments growing out from a carpogonium or from an auxiliary cell may lie free from one another, or they may be compacted into a pseudoparenchymatous mass. All the cells of a gominoblast filament, or the terminal cells only, may enlarge to form what are usually termed the "carpospores." When fully mature, they generally, if not always, have an escape of the protoplast from the surrounding wall[3] Hence the so-called carpospore is really a sporangium (*carposporangium*) and the naked protoplast is the real carpospore. Carposporangia of almost all Florideae contain one carpospore each, but there are a few species (as *Lnagora tetrasporifera* Børgesen)[4] in which each carposporangium contains four carpospores (Fig. 173*F*).

[1] Drew, 1934 [2] Kylin, 1928. [3] Kylin, 1917*A*.
[4] Børgesen, 1927; Kylin, 1930.

The mass of carposporangia, the sterile cells of the gonimoblast filaments, and the cell or cells subtending the gonimoblast filaments jointly constitute the fruiting body or *cystocarp*. It may be borne freely exposed, or it may be protected by surrounding vegetative tissues. In some cases protection results from an embedding of the cystocarp in the thallus; in other cases its protection is due to an upward growth of underlying vegetative tissue into an urn-shaped sheath, the *pericarp*.

Nature of the Cystocarp. All of the older and many of the present-day phycologists interpret the cystocarp as an integral portion of the thallus producing it. Some 40 years ago Oltmanns[1] proposed an entirely different conception of the cystocarp. He suggested that, when interpreted from the morphological standpoint, the cystocarp is really an asexual spore-producing generation parasitic upon the thallus bearing the sex organs. Oltmann's theory was quite generally ignored when first proposed, but in recent years a number of phycologists have accepted it. Their adherence to the theory during the past decade is best shown by their substitution of the term *carposporophyte* for cystocarp.

Germination of Carpospores. Carpospores produced by a carposporophyte may be haploid or diploid. Germinating haploid carpospores always develop into gametophytes which produce sex organs.

Diploid carpospores liberated from a carposporophyte develop into a free-living, asexual, diploid plant (the *tetrasporophyte*) which produces *tetraspores*. This has been culturally demonstrated for a few species with diploid carpospores[2] and is universally assumed to be true for all of them. The tetrasporophyte is usually identical with the gametophyte in appearance and structure, but there are a few species in which there are some structural differences.[3]

Tetrasporophytes (except for aberrant individuals of certain species) produce only sporangia. The most characteristic of these is the *tetrasporangium*. Tetrasporangia may be borne superficially or internally and isolated from one another or in nemathecia. Young tetrasporangia of almost all species are uninucleate, and, in all[4] but one[5] of the cytologically investigated cases, this nucleus divides meiotically into four haploid nuclei. Young tetrasporangia of certain species contain several nuclei,[6] but all except one of them degenerate; it divides meiotically. Meiosis is followed by a cytokinesis that divides the sporangial protoplast into four haploid *tetraspores*. Tetraspores of a few species are known[7] to develop into gametophytes, and this is assumed to be true for all other species.

[1] Oltmanns, 1898. [2] Lewis, 1912, 1914. [3] Howe, 1917, 1918.
[4] Kylin, 1914, 1916; Lewis, 1909; Svedelius, 1914; Yamanouchi, 1906, 1921.
[5] Svedelius, 1935. [6] Svedelius, 1914*A*. [7] Drew, 1934; Lewis, 1912, 1914.

Tetrasporophytes may also produce paraspores.[1] These are generally borne within sporangia whose walls are structurally different from those of tetrasporangia. The number of paraspores within the *parasporangia* borne by a single plant varies considerably. Parasporangia of most species contain 20 to 30 paraspores (Fig 189), but they may contain only one or two. It has been assumed[2] that the paraspores are diploid and that they always germinate to form new tetrasporophytes. It is very probable that this assumption is correct, but as yet there are neither cytological nor cultural data confirming it.

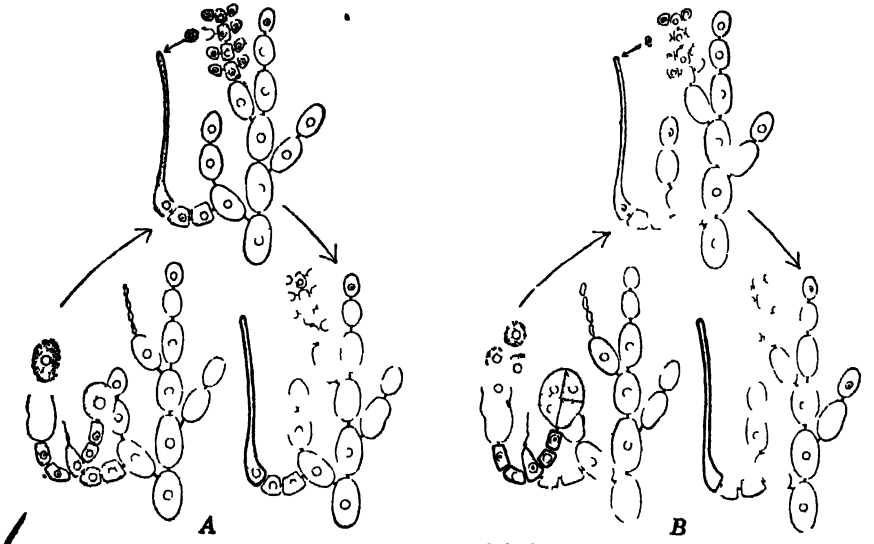


FIG. 167.—Diagrams showing the two types of diphasic cycle found among the Rhodophyceae. Diploid cells in the cycle are outlined with a heavy line. *A*, the cycle in which a haploid carposporophyte alternates with the gametophyte. *B*, the cycle in which a diploid carposporophyte alternates with the gametophyte.

Alternation of Generations in Florideae. Some of the Florideae have a biphasic alternation of generations in which the sexual plant (the gametophyte) alternates with a parasitic asexual plant (the carposporophyte). Others are triphasic with the three generations (gametophyte, carposporophyte, tetrasporophyte) successively following one another. The Florideae also differ from other plants in that alternation of generations is not always accompanied by an alternation in number of chromosomes. Consequently the following three types of life cycle may be recognized among the Florideae: a biphasic alternation of a gametophyte and a haploid carposporophyte; a biphasic alternation of a gametophyte and a diploid carposporophyte; and a triphasic cycle in which both carposporophyte and tetrasporophyte are diploid.

[1] Kolderup-Rosenvinge, 1909–1924; Schiller, 1913.

[2] Kolderup-Rosenvinge, 1909–1924.

A diphasic alternation of a gametophyte with a haploid carposporophyte (Fig. 167*A*) has been demonstrated cytologically[1] for certain Nemalionales, and there is a strong presumption that it occurs in all other members of the order in which the carposporangium contains but one carpospore.

There appear to be three Florideae in which there is a diphasic alternation of a gametophyte with a diploid carposporophyte (Fig. 167*B*). *Liagora tetrasporifera* Børgesen has a carposporophyte similar in appearance to other species of the genus, but one in which the carposporangia

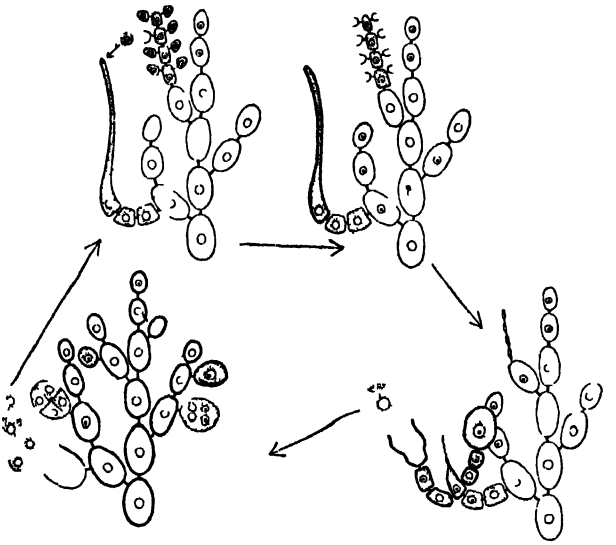


FIG. 168.—Diagram of the triphasic life cycle among Rhodophyceae in which a gametophyte, a diploid carposporophyte, and a tetrasporophyte successively follow one another. Diploid cells in the cycle are outlined with a heavy line

each contain four carpospores. It is generally assumed[2] that the nucleus in the carposporangium divides meiotically, but this has never been demonstrated cytologically. This assumption is based upon the tetraspore-like appearance of the four carpospores within a carposporangium.

The other two diphasic species with a gametophyte and a diploid carposporophyte seem to be derived from an ancestor with a triphasic cycle. *Phyllophora Brodiaei* (Turn.) J Ag.[3] has a gametophyte with normal sex organs and a development of filaments from an auxiliary cell (the supporting cell of a carpogonial branch).[3] Cells toward the free ends of many of the filaments become sporangia, each containing four spores, and it has been shown[4] that spore formation is preceded by meiosis. The diploid nature of the filaments is unquestioned, but

[1] Cleland, 1919; Kylin, 1916*B*, 1917; Svedelius, 1915, 1933.

[2] Børgesen, 1927; Kylin, 1930*A*; Svedelius, 1931.

[3] Kolderup-Rosenvinge, 1929. [4] Claussen, 1929.

this plexus of filaments has been considered[1] a reduced parasitic tetrasporophyte rather than a carposporophyte. The warty, excrescent, tetraspore-producing mass does not look like a carposporophyte, but it should be considered one because it remains in organic connection with an auxiliary cell which is an integral part of the gametophyte. Other species of *Phyllophora* are known to be triphasic, and it is very probable that the diphasic cycle of *P. Brodiaei* arose through a pushing back of meiosis to the carposporangium, coupled with a complete dropping of the tetrasporophyte from the triphasic life cycle. The life cycle of *Gymnogongrus Griffithsiae* Mart. has recently been found[2] to be quite similar to that of *P. Brodiaei*.

All of the species with a free-living tetrasporophyte are triphasic and with the gametophyte successively followed by a diploid carposporophyte and a diploid tetrasporophyte (Fig. 168).

Evolution within the Florideae. With one exception,[3] all present-day phycologists hold that the Nemalionales in which meiosis immediately follows syngamy are the most primitive of all Florideae. The fundamental feature in an advance from this condition has been a postponement of the time at which meiosis takes place.[4] The first step was a postponement of meiosis to the time of carpospore formation. This resulted in a diphasic alternation of a gametophyte and a diploid carposporophyte. The next step was an omission of meiosis in the carposporangium and a consequent production of diploid carpospores. This evolution of diploid carpospores did not involve an introduction of new genes, and as a result the free-living diploid plants evolved from them were identical in vegetative structure with those developed from haploid carpospores. Thus the free-living diploid generation is to be interpreted as homologous with and not antithetic to the haploid generation. The diploid generation thus evolved lacked sex organs and produced sporangia only. These sporangia seem to be homologous with monosporangia of gametophytes[5] but differ from them in that the single nucleus divides meiotically and the sporangial protoplast divides to form four haploid tetraspores.

The most primitive of the Florideae with a free-living tetrasporophyte undoubtedly had (as in the present-day Gelidiales) the carposporophyte growing directly from the carpogonium. When the carposporophyte develops upon a carpogonial branch, the amount of available food is limited. A much greater supply of food is available when the carposporophyte is borne upon other parts of the plant. Thus the auxiliary cell must be looked upon as a secondary feature and one that arose in connection with nutrition of the developing carposporophyte.

[1] Kolderup-Rosenvinge, 1929; Svedelius, 1931.
[2] Chemin, 1933; Gregory, 1934. [3] Tilden, 1935.
[4] Cleland, 1919; Svedelius, 1927, 1931. [5] Cleland, 1919.

Classification. The Florideae were classified according to various bases until Schmitz[1] showed that the most important character in a natural classification is the structure and development of the cystocarp (carposporophyte). The determination of the proper systematic disposition of the many genera of the Florideae has involved a tremendous amount of detailed investigation, and it is largely through the efforts of Kylin and his students[2] that Schmitz's system has been refined into its present form which divides the Florideae into six orders.

ORDER 1. NEMALIONALES

The Nemalionales differ from all other Florideae in their lack of a tetrasporophytic generation. Almost all genera have the carposporophyte developing from the carpogonium, but there are genera[3] in which there is an auxiliary cell. One species seems to have meiosis delayed until the time of carpospore formation; all others have it immediately following gametic union. The order contains some 35 genera and 250 species. These have been divided[4] into seven families.

Nemalion is a marine summer annual which grows in the midlittoral zone. It is rather localized in distribution, but there are usually many individuals at stations where it does grow. The plant body is cylindrical, sparingly to profusely branched, gelatinous in texture, and of a reddish-brown color (Fig. 169*A*). The generic name is based upon the distinctly worm-like appearance of the thalli as they lie clinging to rocks when the tide is out.

The carpospore is naked when liberated from a carposporangium, but it becomes invested with a wall about the time it becomes affixed to a rock or some other firm substratum. Its germination begins with the protrusion of a germ tube and a migration of the chromatophore and most of the cytoplasm into the tube. The nucleus moves to the base of the tube and there divides. One daughter nucleus remains within the old spore wall; the other migrates into the tube.[5] A cross wall is then formed at the base of the tube, and the cell thus cut off functions as an apical cell. Division and redivision of the apical cell produces a protonema-like, sparingly branched, monoaxial filament with a dozen or more cells.[6] Lateral branches of the protonema become intertwined with one another and develop into the adult portion of the plant body. This is multiaxial in organization and with many apical cells at the growing tip (*cf. Cumagloia*, Fig. 170*B*).

[1] Schmitz, 1889.
[2] Bliding, 1928; Kylin, 1923, 1928, 1930*A*, 1935; Sjostedt, 1926.
[3] Svedelius, 1933. [4] Kylin, 1932.
[5] Cleland, 1919; Lewis, 1912*A*. [6] Chester, 1896; Kylin, 1917*A*.

Mature portions of the plant body are differentiated into a colorless axial core and a colored ensheathing layer. The mature portion of the axial core is composed of closely intertwined longitudinal filaments of elongate cells without chromatophores or nuclei.[1] The ensheathing layer, often called the cortex, consists of short, erect, densely branched, lateral filaments terminating in elongate hyaline hairs. Median cells of lateral filaments are barrel-shaped, uninucleate, and have a single stellate chromatophore containing a conspicuous pyrenoid.

Nemalion is homothallic, but many plants appear to be heterothallic because there is not a simultaneous production of the two kinds of sex organs. The initial of a spermatangial branch is an ordinary vegetative cell terminating a lateral filament from the central core. This initial cuts off a chain of four to seven derivatives each of which is a spermatangial mother cell. Spermatangial branches are easily distinguishable from vegetative ones because their cells are colorless or have feebly developed chromatophores. Each spermatangial mother cell[2] generally buds off four radially disposed spermatangia (Fig. 169*B*). The spermatium within a spermatangium contains a single nucleus and a rudimentary chromatophore. It is liberated by a rupture of the spermatangial wall, and, after its escape, a new spermatangium may develop within the old spermatangial wall.

The carpogonial filament is developed from an initial cell borne near the base of a lateral filament from the central core. The initial functions as an apical cell that usually cuts off three daughter cells, but the number formed may range from one to five. The apical cell of a carpogonial filament becomes the carpogonium after it stops forming daughter cells. The carpogonium has an elongate protuberance, the trichogyne, at the distal end (Fig. 169*C–D*). Most carpogonia of *Nemalion* are uninucleate, but occasional ones are binucleate, with an ephemeral nucleus in the trichogyne.[1]

Spermatia carried about by water currents may lodge against a trichogyne. A spermatium is uninucleate at the time of lodgment but shortly afterward its nucleus divides into two daughter nuclei.[1] This is followed by a dissolution of spermatial and trichogynal walls at the point of mutual contact and a migration of one or both spermatial nuclei into the trichogyne. One of the spermatial nuclei migrates to the carpogonial base, where it unites with the female nucleus.

The zygote nucleus increases in size and then divides meiotically into two daughter nuclei which lie one above the other. There is next a formation of a horizontal wall between the two nuclei (Fig. 169*E*). The nucleus within the inferior daughter cell eventually disintegrates. That within the superior daughter cell of the carpogonium divides equationally,

[1] Cleland, 1919. [2] Cleland, 1919; Kylin, 1916*B*; Wolf, 1904.

and one daughter nucleus moves into a lateral protuberance growing out from the cell. A vertical wall is formed across the base of the protuberance, and the cell thus cut off is the initial of a gonimoblast filament.

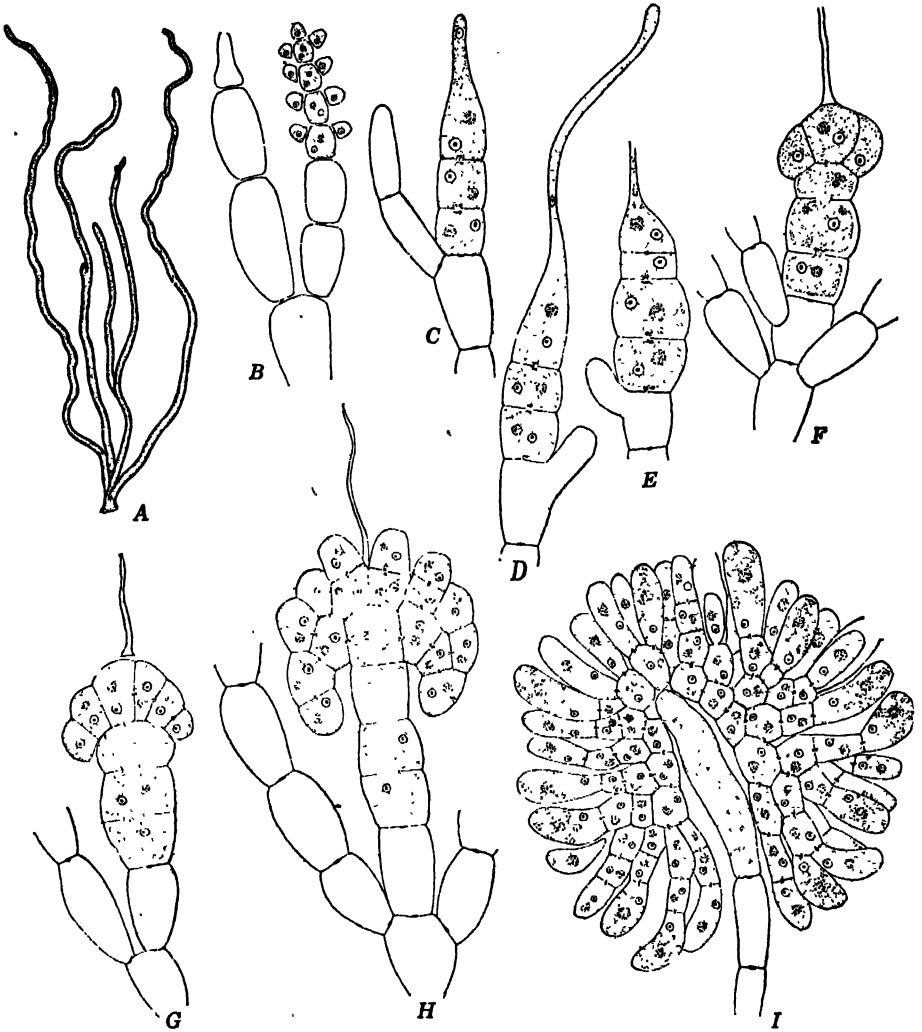


FIG. 169.—*Nemalion multifidum* (Webb. and Morh.) J. G. Ag. *A*, gametophyte. *B*, filament with spermatangia. *C–D*, young and mature carpogonial filaments. *E–H*, early developmental stages of carposporophytes. *I*, mature carposporophyte. (*A*, × ⅓; *B–H*, × 975; *I*, × 650.)

Several additional initials are successively developed in the same manner lateral to the superior cell (Fig. 169*F–G*). Each initial gives rise to a short, compactly branched, gonimoblast filament in which the terminal cell of each branchlet eventually enlarges and becomes a carposporangium.

The gonimoblast filaments jointly constitute the gonimoblast or carposporophyte. Food for development of the carposporophyte is obtained from an elongate *placental cell* produced by terminal fusion of the carpogonial filament cells and the inferior daughter cell of the carpogonium (Fig. 169 *H–I*). The wall of a mature carposporangium ruptures at the distal end, and the carpospore escapes. Liberation of the carpospore may be followed by proliferation of a new carposporangium within the old empty carposporangial wall, and several successive sporangia may be proliferated as the growing season progresses.[1]

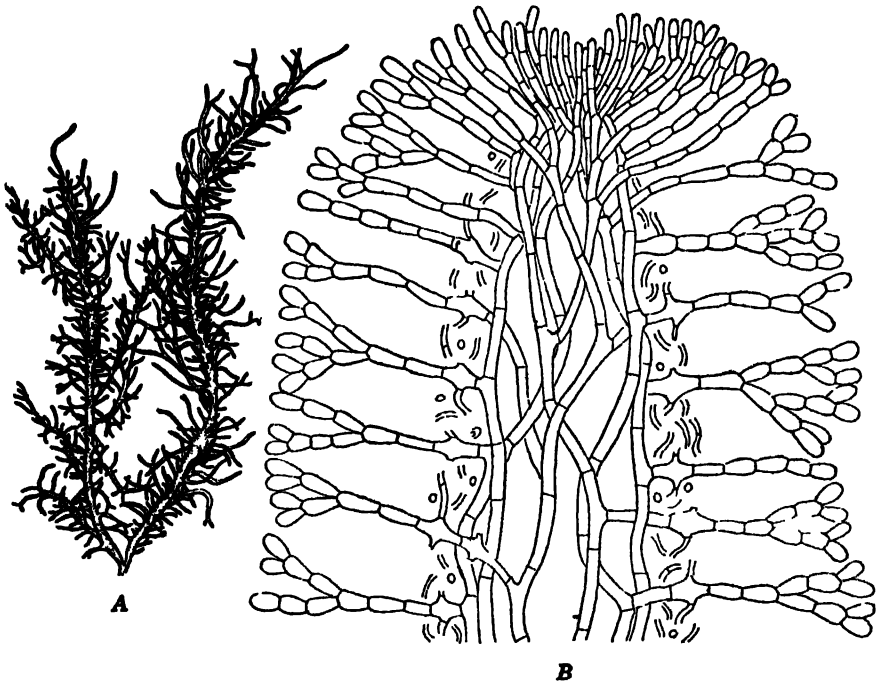


FIG. 170.—*Cumagloia Andersonii* (Farlow) Setchell and Gardne, *A*, gametophyte. *B*, semidiagrammatic vertical section of a branch apex. (*A*, × ½, *B*, × 325.)

Late in the autumn thalli of *Nemalion* disappear completely, and new ones do not reappear until late in the next spring. The prostrate protonematal stage has been found during the winter,[2] and it is very probable that the plant remains in this stage of development during the winter.

Cumagloia, with the single species *C. Andersonii* (Farlow) Setch. and Gardn., is widespread along the Pacific Coast of the United States. It, also, is a summer annual which disappears about the first of November and reappears about the first of May. The adult thallus[3] has a disk-shaped holdfast bearing a simple or sparingly forked blade with innumer-

[1] Cleland, 1919; Kylin, 1916*B*; Wolf, 1904.
[2] Kolderup-Rosenvinge, 1909–1924. [3] Gardner, 1917.

able delicate cylindrical proliferations (Fig. 170*A*). The growing point has a group of apical initials. The mature region has a central core of longitudinal filaments ensheathed by a layer of erect assimilating filaments (Fig. 170*B*). The assimilating filaments are more sparingly branched than those of *Nemalion*, and they do not terminate in hairs. Cells of the assimilating filaments are uninucleate and have a single stellate chromatophore.

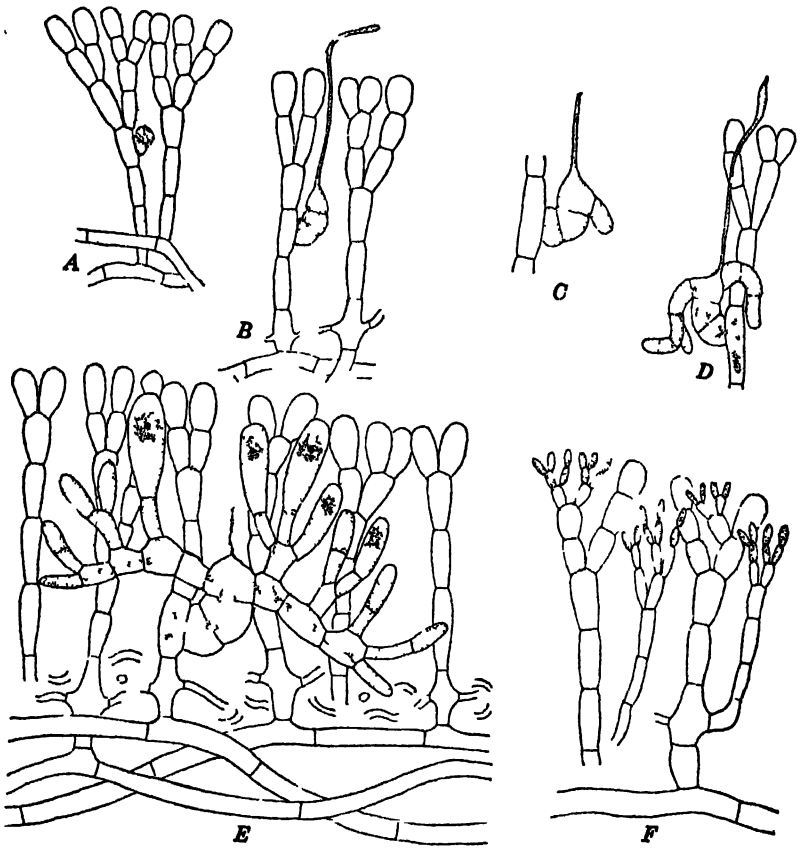


FIG. 171 —*Cumagloia Andersonii* (Farlow) Setchell and Gardner *A–B*, young and mature carpogonial filaments *C–D*, carpogonium with young gonimoblast filaments. *E*, carposporophyte with carposporangia. *F*, spermatangia. (× 430)

Most thalli bear only one kind of sex organs, but occasional ones bear both kinds. The spermatangia are borne in small clusters at the tips of assimilating filaments (Fig. 171*F*). Carpogonial filaments are differentiated close to the growing apex and laterally upon the assimilating filaments. They are generally three-celled. The terminal cell develops into a carpogonium whose elongate trichogyne projects beyond the thallus (Fig. 171*A–B*). Fertilization is effected in the usual manner, and it is

thought that there is an immediate reduction division of the zygote nucleus. Initials of gonimoblast filaments are cut off directly from the carpogonium and not from a daughter cell of it as in *Nemalion* (Fig. 171*C–D*). Gonimoblast filaments developed from the initials extend horizontally from the carpogonium and grow between the assimilating filaments. They produce numerous short erect branchlets toward the thallus exterior, and the terminal cell of each branchlet develops into a large elongate carposporangium.[1] The mature carposporophyte (Fig. 171*E*) is a diffuse filamentous structure instead of a compact globose mass as in most other Nemalionales. The production of carposporangia is long continued, and new ones are successively proliferated within old empty sporangial walls that have discharged their carpospores. Food for growth of the carposporophyte is obtained from the carpogonial filament. Its cells become much larger and have much broader cytoplasmic connections than at the time of fertilization.

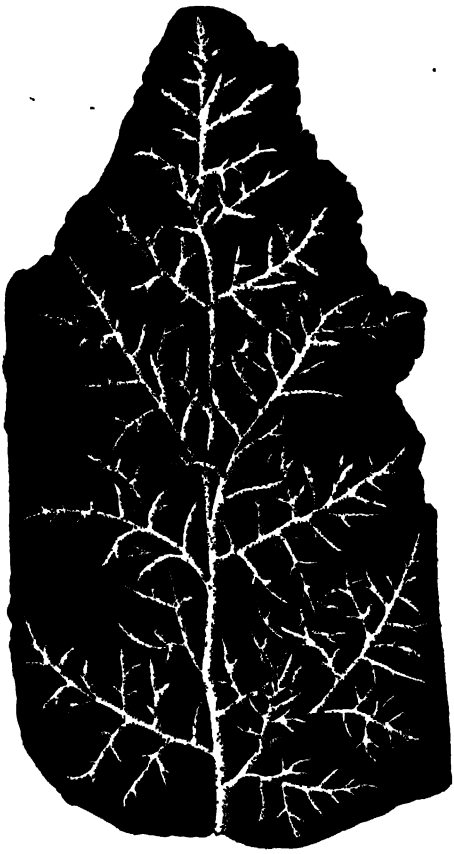


FIG. 172.—*Liagora pinnata* Harvey. (× 1½.)

Liagora is a genus with 20 or more species, all of which are tropical or subtropical in distribution. Thalli of *Liagora* are profusely branched cylinders 5 to 20 cm. in height. According to the species, the branching is predominantly dichotomous or monopodial. The gelatinous matrix of the thallus is always calcified, and the calcification may be so extensive that the thalli are whitish in color and of a brittle, chalky texture (Fig. 172). The vegetative structure is similar to that of *Nemalion* and *Cumagloia*.

Most of the species are homothallic. The spermatangia are borne in globular or flattened clusters toward the extremities of assimilating filaments (Fig. 173*E*). The carpogonial filaments (Fig. 173*A–B*) are three- to six-celled and borne laterally low on the assimilating filaments.[2]

[1] Gardner, 1917; Kylin, 1928. [2] Børgesen, 1915, 1927; Kylin, 1930*A*.

Fertilization of *L. viscida* (Forsk.) C.A.Ag. is followed by a transverse division of the carpogonium and a development of gonimoblast filaments from the superior daughter cell.[1] The gonimoblast filaments grow radially outward and lie intermingled with the assimilative filaments (Fig. 173*C–D*). Only the terminal cells of gonimoblast filaments develop into carposporangia.

L. tetrasporifera Børgesen has a carposporophyte different from that of any other species. Its carpogonial filaments are three- or four-celled. The carpogonium divides transversely after fertilization, and the gonimoblast filaments grow outward from the superior daughter cell. They are more densely compact and have broader cells than those of *L. viscida*.[1]

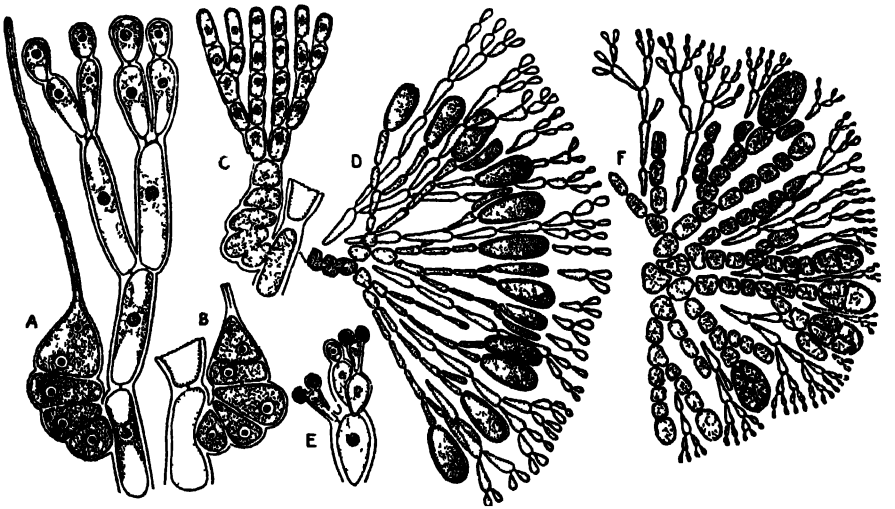


FIG. 173 —*A, E, Liagora viscida* (Forsk.) C.A.Ag. *A*, carpogonial filament. *B*, carpogonium after the first division. *C*, young carposporophyte. *D*, mature carposporophyte. *E*, spermatangia. *F*, mature carposporophyte of *L. tetrasporifera* Børgesen. (*From Kylin*, 1930*A*.) (*A, B*, × 800; *C*, × 540; *D*, × 360; *E*, × 316.)

L. tetrasporifera[2] differs from other species in that four carpospores are formed within each carposporangium (Fig 173*F*). Material has not been available for a cytological investigation of carpospore formation, but there is a general belief[3] that meiosis is delayed until the time the carpospores are formed. The chief basis for this belief is the similarity in appearance of these carposporangia and tetrasporangia of genera with tetrasporophytes. If this assumption is correct, *L. tetrasporifera* has an unusual life cycle in which there is a biphasic alternation of a haploid gametophyte with a diploid carposporophyte.

Scinaia is one of the few Nemalionales in which the carposporophyte is surrounded by a pericarp. It is also of interest because it is the genus

[1] Kylin, 1930*A*. [2] Børgesen, 1927; Kylin, 1930*A*.
[3] Børgesen, 1927; Kylin, 1930*A*; Svedelius, 1931.

where meiosis was first demonstrated among the Rhodophyta.[1] *Scinaia* is a marine genus of world-wide distribution. There are about a dozen species.[2] Two of them have been recorded from the Atlantic Coast of this country and one from the Pacific Coast. All three are rare algae.

The thallus is erect, is cylindrical to subcylindrical, and has several successive dichotomous branchings (Fig. 174). The growing points are multiaxial and have many apical cells. Mature regions of a thallus have an axial core of colorless longitudinal filaments. The axial core is surrounded by an encircling layer of corymbosely branched filaments that stand vertical to it. The outermost branchlets of the corymbose filaments are compacted into a pseudoparenchymatous tissue whose cells

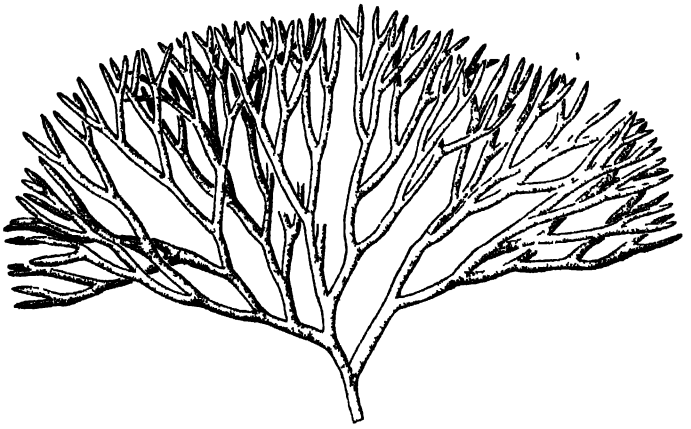


FIG. 174.—Gametophyte of *Scinaia furcellata* (Turn.) Bivona. (Natural size.)

contain chromatophores. Terminal cells of many of the branchlets enlarge to several times their original size and become colorless (Fig. 175*A*). These cells constitute the colorless epidermis-like layer at the surface of a thallus.[3]

The gametophyte of *Scinaia* reproduces asexually by means of monospores.[1] They are formed in monosporangia borne at the tips of branchlets which have grown out between the "epidermal" cells. The terminal cell of a branchlet is a mother cell which buds off either one or two monosporangia (Fig. 175*C*). A monosporangium contains a single haploid nucleus, and the entire protoplast becomes the naked monospore that is liberated by rupture of the sporangial wall. Liberation of the monospore may be followed by proliferation of a new monosporangium within the old sporangial wall.[1] The method of germination of monospores is unknown.

Gametophytes of *Scinaia* may be homothallic or heterothallic. The spermatangia lie in large or small sori scattered over the thallus surface. They are borne upon branchlets of filaments which grow up between and

[1] Svedelius, 1915. [2] Setchell, 1914. [3] Setchell, 1914; Svedelius, 1915.

project beyond the "epidermal" cells [1] The terminal cell of each projecting branchlet is a spermatangial mother cell that bears two or three spermatangia at the distal end Each spermatangium contains a single spermatium which is liberated by a rupture of the spermatangial wall (Fig 175*D*). Development of spermatangia may continue for some time, because new spermatangia may be proliferated within walls of old empty ones.

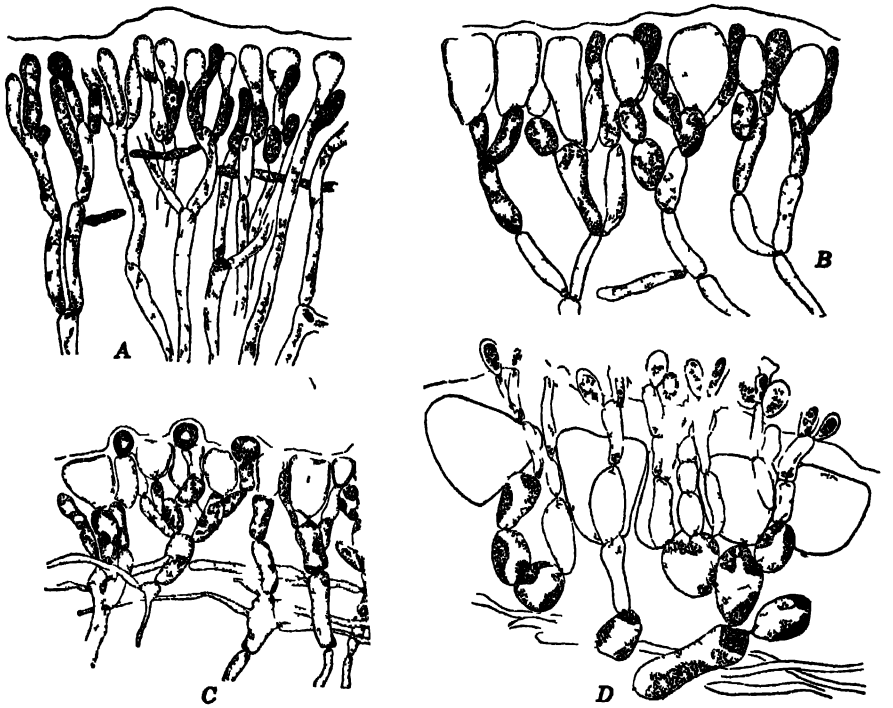


FIG 175 —*Scinaia furcellata* (Turn) Bivona *A* section of vegetative region with young epidermal cells *B* the same with mature epidermal cells *C* monosporangia *D* spermatangia (*From Svedelius* 1915) (*A B* × 615 *C* × 510 *D* × 600)

Carpogonial filaments are formed close to the growing apex and upon vertical filaments from the central axis (Fig 176 1) A carpogonial filament is three-celled and has the terminal cell metamorphosing into a carpogonium with a long trichogyne *Scinaia* is one of the few Florideae where there is a nucleus both in the trichogyne and in the carpogonial base.[1] Shortly before fertilization the median cell of a carpogonial filament cuts off four large cruciately disposed *nurse cells*, each densely filled with protoplasm (Fig 176*B*) At the same time there is a development of upwardly curved sterile filaments from the lowermost carpogonial filament cell These curved filaments become the urn-shaped pericarp

[1] Svedelius, 1915

which surrounds the mature carposporophyte. A mature pericarp lies embedded just within the thallus surface, and it has an opening, the ostiole, at the distal end

Immediately after fertilization there is a migration of the zygote nucleus into one of the nurse cells (Fig 176*C*) There it divides meiotic-

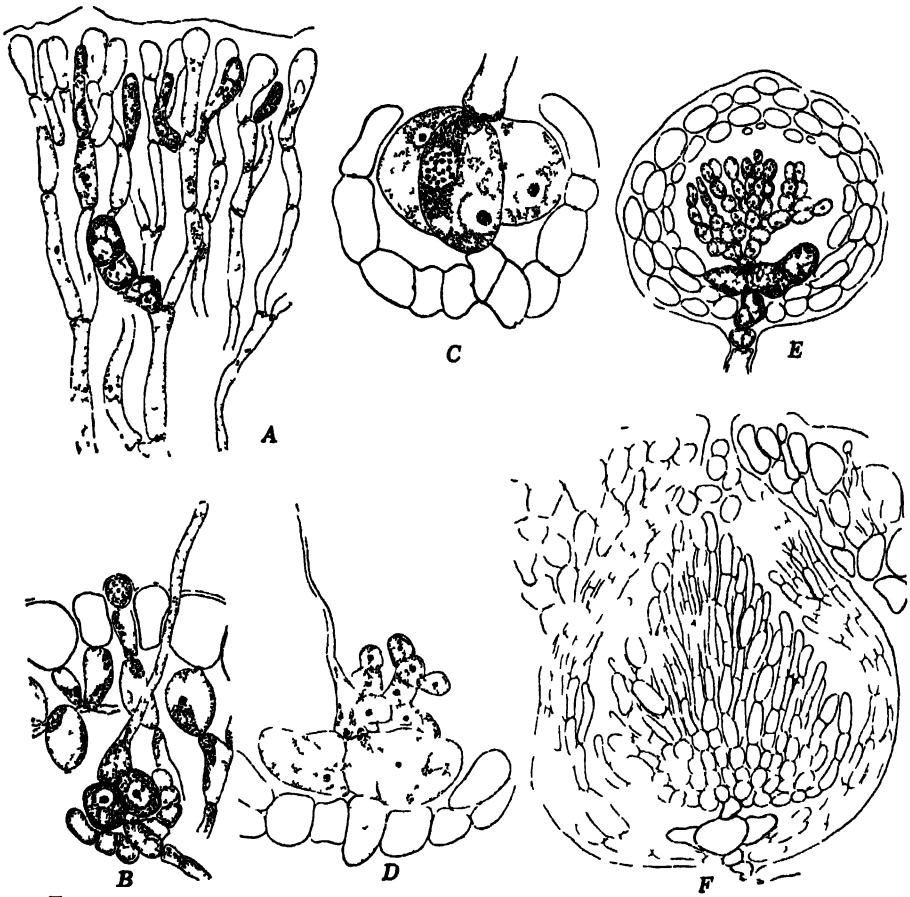


FIG 176 — *Scinaia furcellata* (Turn) Bivona 1 *B* young and mature carpogonial filament *C*, after migration of the zygote nucleus into one of the nurse cells *D E* early stages in development of carposporophytes *F* mature carposporophyte with its surrounding pericarp. (*From Svedelius*, 1915) (1 *B* × 615, *C*, × 1,150, *D*, × 840, *E*, × 345)

ally into four haploid daughter nuclei [1] One of these nuclei migrates into the gonimoblast primordium which grows up through the old empty carpogonium (Fig. 176*D-E*). The gonimoblast primordium develops into an outwardly divergent and profusely branched system of gonimoblast filaments which fill most of the space within the pericarp Three or

[1] Svedelius, 1915

four of the outermost cells of certain branchlets of a gonimoblast filament develop into carposporangia. Other branchlets remain sterile and develop into paraphyses (Fig. 176*F*). The nucleus of the single carpospore within each carposporangium has the haploid number of chromosomes. Eventually there is a liberation of the carpospores by an apical rupturing of the carposporangial wall. Although not demonstrated by cultures, there is every reason for believing that the liberated carpospores develop directly into gametophytes.

ORDER 2. GELIDIALES

The Gelidiales are the only tetrasporophytic Florideae in which the carposporophyte develops directly from the carpogonium. There is but one family, the Gelidiaceae, and it contains about a half dozen genera.

The type genus, *Gelidium*, is a widely distributed marine alga with many species. It is a perennial plant in which new shoots are proliferated from the persisting basal portion each growing season. The thallus is cylindrical or flattened, pinnately branched, and of a tough consistency. In many species the branchlets bend away from the axis in a geniculate fashion and are constricted in the basal portion (Fig. 177*A*).

Gelidium is the chief source of the commercial product known as agar or vegetable isinglass. This substance is widely used in industry as a solidifying agent in foodstuffs, in the sizing of textiles, or in the clarifying of liquids. It is also used as the solidifying agent in a wide variety of culture media in biological laboratories.

Japan produces more than 95 per cent of the agar marketed and in 1933 the annual production was valued[1] at 3,200,000 yen ($1,600,000 at normal exchange). Some of the *Gelidium* used in the manufacture of agar is gathered in the intertidal zone, but most of it is collected by divers. The collectors dry the algae and then sell them to manufacturers of agar. Agar is manufactured during the winter months only and preferably in mountainous regions where the air is dry and pure.[2] The manufacturer of agar removes all foreign matter from the dried algae, washes them in running fresh water, and spreads them out to bleach on bamboo racks. The dried and bleached algae are then boiled in a kettle over a specially constructed furnace. Boiling extracts the vegetable gelatin and this is separated from the pulpy residue by filtering through cloths. The filtered liquid is run into shallow wooden troughs and allowed to cool. After attaining a certain degree of hardness, the cooling mass of jelly is cut into blocks in order to facilitate handling. The blocks may be spread out to dry, or they may be cut into small sticks which are allowed to dry.

Thalli of *Gelidium* have a single apical cell at each branch apex. The derivatives cut off at the posterior face of an apical cell mature into the

[1] Japan, Department of Finance, 1935. [2] Smith, H. M., 1905.

single axial filament of the adult portion (Fig 177*B*). Cells of the axial filament, one or two back from the apical cell, cut off four quadrately arranged pericentral cells and each of them produces a short branched

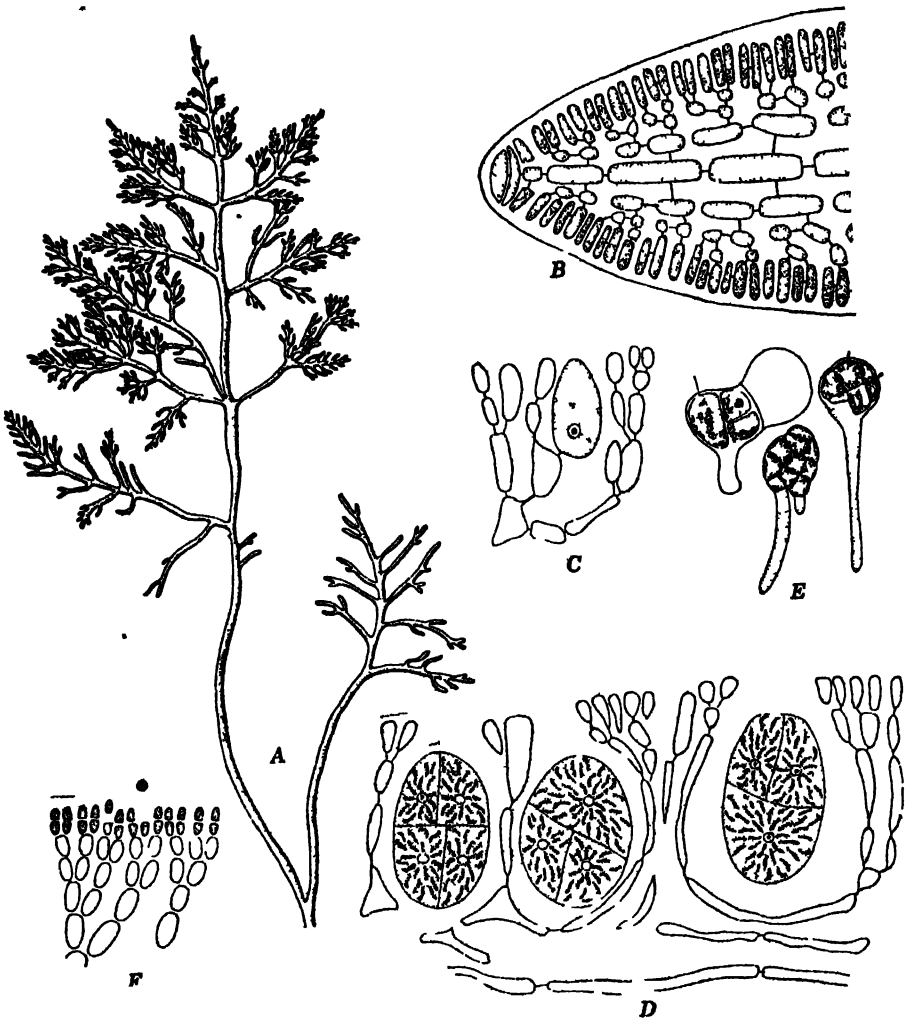


Fig 177.—*A–D, F Gelidium cartilagineum* Gaill *A*, thallus *B*, diagrammatic vertical section of a thallus apex *C–D*, young and mature tetrasporangia *E*, germinating tetraspores of *G capillaceum* (Gmel) Kutz *F* spermatangia (*E, after Kylin*, 1914) (*A*, × ½ *B–D*, × 650, *F*, × 430)

lateral filament [1] The tips of these lateral filaments are compacted into the pseudoparenchymatous tissue which forms the surface of the thallus.

Gelidium differs from most other American Florideae in that the thalli, both sexual and tetrasporic, usually fruit during the late autumn and

[1] Kylin, 1928

winter months. Gametophytes of *G. cartilagineum* Gaill. are heterothallic. The spermatangia are borne in elliptical sori (nemathecia) on the flattened sides of branchlets of male plants (Fig. 177*F*). A spermatangial mother cell usually bears two spermatangia which become transversely divided after they are cut off.[1]

Fertile branches of female gametophytes are macroscopically distinguishable from vegetative branches on account of their indented apices. Carpogonial filaments are developed on the flattened sides of fertile branches and close to the growing point. The carpogonial filament is one-celled, and it is borne upon the lowermost cells of a vegetative fila-

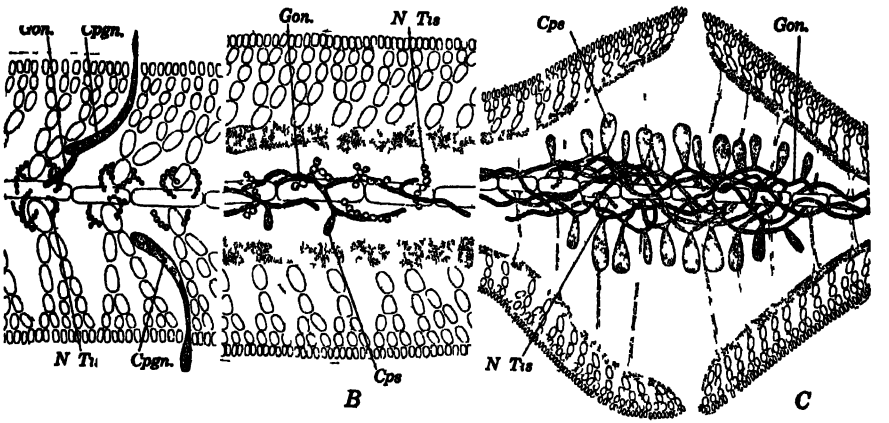


FIG. 178.—*Gelidium cartilagineum* Gaill. Diagrammatic longitudinal sections of thalli with developing carposporophytes. *A*, carpogonium and carpogonium producing first gonimoblast filament. *B*, carposporophyte with very young carposporangia. *C*, carposporophyte with mature carposporangia. (*Cpgn.*, carpogonium; *Cps.*, carposporangium; *Gon.*, gonimoblast filament; *N Tis.*, nurse tissue.) (*A*, *B*, × 300, *C*, × 210.)

ment growing out from the central axis. The single cell of a carpogonial filament metamorphoses into a carpogonium with an elongate trichogyne that is inflated in the distal portion (Fig. 178*A*). Carpogonial development is accompanied by an outgrowth of small-celled filaments from the basal (pericentral) cells[1] of vegetative filaments. The cells of these special filaments are densely packed with protoplasm, and they serve as a nurse tissue for the growing carposporophyte. The gonimoblast filament growing out from the base of a carpogonium is many-celled and sparingly branched. It grows longitudinally along the axial filament and between the nurse filaments (Fig. 178*B*). Eventually it forms numerous erect, one-celled, lateral branchlets which develop into carposporangia (Fig. 178*C*). It is very probable that the interwoven mass of gonimoblast filaments about an axial filament has grown out from several carpogonia. Thus the "cystocarp" of *Gelidium* is to be interpreted as an aggregation

[1] Kylin, 1928.

of carposporophytes rather than as a single one. Development of the carposporangia is accompanied by an upward arching of the overlying tissues and differentiation of an opening (ostiole) in one or in both of the flattened sides. Carpospores liberated from the carposporangia float out through these pores and are carried about by water currents.

Germlings produced by germination of carpospores have not been grown to maturity, but there is no doubt that they develop into tetrasporophytes. Mature tetrasporophytes of *Gelidium* are indistinguishable from mature gametophytes when the two are in a sterile condition. Fruiting tetrasporophytes may be distinguished by their swollen fertile branchlets. The tetrasporangia lie close to one another along the flattened side of fertile branchlets, but they are not organized into nemathecia. The tetrasporangia are superficial in position when first differentiated, but they gradually become embedded in the thallus through an upgrowth of adjoining vegetative tissue (Fig. 177*C–D*). A young tetrasporangium enlarges to several times its original size, and the nucleus within it divides to form four daughter nuclei. Undoubtedly, as is known for several other tetrasporophytic Florideae, this nuclear division is reductional. The four-nucleate protoplast within a tetrasporangium divides quadrately into four tetraspores which are liberated by a gelatinization of the sporangial wall.

The liberated tetraspore is naked, but it is enclosed by a wall at the time of germination. This begins with a protrusion of the entire protoplast and a formation of a transverse wall separating the protrusion from the old empty spore wall.[1] The protruded cell divides transversely and one of the daughter cells sends out a long colorless rhizoid (Fig. 177*E*). The two successive diagonal divisions of the cell with the rhizoid, or of its sister cell, produce an apical cell which continues all further growth of the new gametophyte.

ORDER 3. CRYPTONEMIALES

The Cryptonemiales are the only tetrasporophytic Florideae with an auxiliary cell borne in a special filament of the gametophyte. Filaments producing the auxiliary cells are markedly different from vegetative filaments. The order contains some 85 genera and 650 species. They have been divided[2] into nine families, differing from one another in the position of auxiliary cells, in the thallus structure, and in the structure of the carposporophyte.

Filaments with auxiliary cells resemble carpogonial filaments in that their cells lack chromatophores and are densely filled with protoplasm. Thus they appear to be modified carpogonial filaments. However, the

[1] Killian, 1914. [2] Kylin, 1932.

carpogonium and the auxiliary cell cannot be considered homologous,[1] because the former is always terminal in position and the latter is always intercalary

Cryptosiphonia is a marine genus found only in the Pacific Ocean. There are two species, one of which, *C Woodii* J Ag , is widespread along the coast of California The thallus is a slightly compressed sparingly branched cylinder with numerous short, pinnately disposed branchlets on the major branches (Fig 179*A*) A branch tip has a single apical cell.

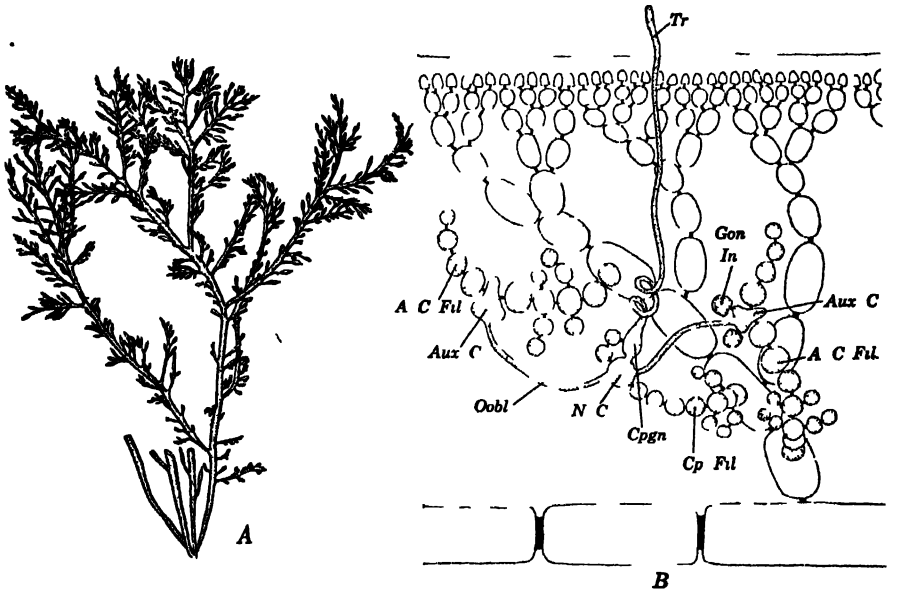


Fig 179 *Cryptosiphonia Woodii* J G Ag *A* fruiting female gametophyte *B*, diagrammatic longitudinal section of a fertile branch in which a carpogonium has fused with a nurse cell and then sent oöblast filaments to two auxiliary cell filaments (*Aux C*, auxiliary cell *A C Fil* auxiliary cell filament *Cpgn* carpogonium *Cp Fil* carpogonial filament *Gon In* gonimoblast initial *N C* nurse cell *Oöl*, oöblast *Tr* trichogyne) (*A* × $\frac{1}{2}$ *B*, × 325)

Each axial cell cut off posterior to the apical cell forms two *pericentral cells* that lie at an angle of 90 degrees to each other[2] The pairs of pericentral cells borne on successive axial filament cells alternate with one another. Each pericentral cell gives rise to a filament in which all secondary branchlets lie close to one another. Thus, mature portions of a thallus have an outer pseudoparenchymatous tissue surrounding an inner, loosely branched tissue with a single conspicuous axial filament.

The structure of the spermatangia is as yet unknown. Fruiting female gametophytes are macroscopically recognizable because of the spindle-shaped fertile branchlets Both the carpogonial and the auxiliary

[1] Kylin, 1930*A* [2] Kylin, 1930*A*; Sjostedt, 1926

cell filaments develop on the adaxial face of lateral filaments from the pericentral cells (Fig. 179*B*). The carpogonial filaments differ from those of most other Florideae in that they are 7 to 10 cells in length and have lateral branchlets from the lowermost cells.[1] The terminal cell of a carpogonial filament becomes a carpogonium with a very long trichogyne whose basal portion has a couple of spiral turns (Fig. 180*A*). The apex of the carpogonial filament is always recurved in such a manner that the carpogonial base adjoins the third cell below it. This is the *nurse cell.*

After fertilization there is a fusion of the carpogonial base with the nurse cell (Fig. 180*B*). Certain other Cryptonemiales are known[2] to

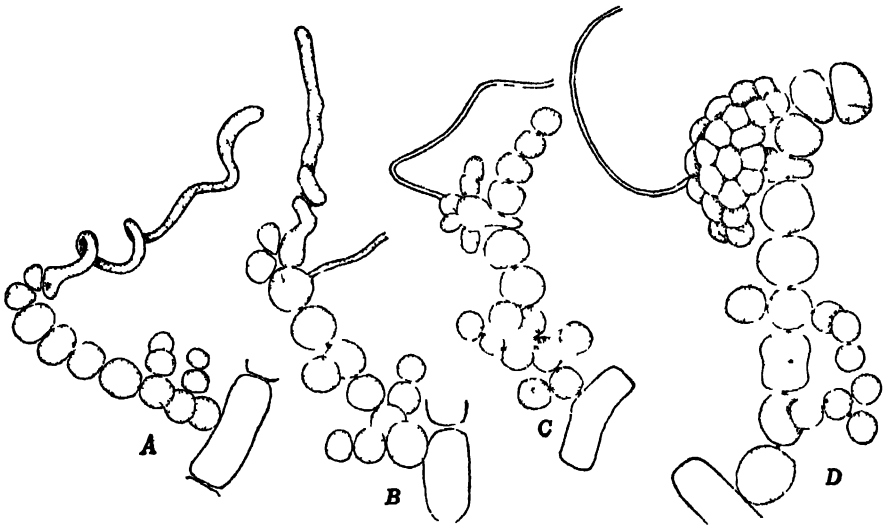


FIG. 180.—*Cryptosiphonia Woodii* J G Ag *A*, carpogonial filament before fusion of carpogonium and nurse cell *B*, carpogonial filament after fusion of carpogonium and nurse cell, and after sending forth of ooblast *C D*, auxiliary cell filaments with young and old carposporophytes growing from the auxiliary cell Note that the carposporophyte develops on the side of an auxiliary cell fused with the ooblast. (× 350.)

have a migration of the zygote nucleus, or one of its daughter nuclei, into the nurse cell, and it is very probable that the same is true for *Cryptosiphonia.* The nurse cell then sends forth a tubular outgrowth, the *ooblast,* which grows to, and fuses with, one of the medial intercalary cells of an auxiliary cell branch. Three or four of the median cells of the branch are potential auxiliary cells, but only one of them is functional. It is thought that a diploid nucleus migrates to the auxiliary cell through the ooblast. The auxiliary cell next produces gonimoblast filaments from the side that the ooblast entered (Fig. 180*C-D*). An auxiliary cell may begin to develop gonimoblast filaments immediately after it receives a diploid nucleus, or it may send out a secondary ooblast that grows to

[1] Kylin, 1930*A*; Sjostedt, 1926 [2] Kylin, 1928, 1930*A*; Oltmanns, 1898.

another auxiliary cell branch. Thus more than one carposporophyte may be produced as a result of a single gametic union. The carposporophyte consists of a compactly branched mass of gonimoblast filaments in which each cell eventually develops into a carposporangium. Sooner or later there is a disintegration of vegetative tissues external to the carposporophytes. This exposes the carposporangia and permits dispersal of the carpospores liberated from them.

Tetrasporophytes have their tetrasporangia embedded just within the thallus surface. The protoplasts of tetrasporangia divide to form four quadrately disposed tetraspores.

The *Corallinaceae* are Cryptonemiales in which the plant body is strongly calcified. Some genera have a crustose thallus which is entirely calcified; other genera have an erect jointed thallus in which the internodes are calcified and the nodes uncalcified. It is now known[1] that calcareous algae contribute more to the upbuilding of coral reefs than do the coral polyps and other animals. These calcareous algae include the Corallinaceae and certain siphonaceous Chlorophyceae, but the former are by far the most important as reef builders.

Lithothamnion, one of the crustose Corallinaceae, is a large genus with some 125 species. Most of them grow upon rocks, but certain species, including *L. membranaceum* (Esper) Foslie [*Epilithon membranaceum* (Esper) Heydrich] and *L. mediocre* (Foslie) Foslie and Nichols, grow epiphytically upon various algae and upon the leaves of marine angiosperms. The thalli of *L. membranaceum* and *L. mediocre* are circular in outline, are 3 to 8 mm. in diameter, and have the cells radiating from a common center. Sterile thalli of these species are monostromatic at the margin and distromatic at the center. Fruiting thalli are several cells in thickness and with the cells in vertical rows. In *L. membranaceum* the increase in thickness has been shown[2] to be due to division of the lower cell in distromatic portions of a thallus. Thus, growth of the vertical filaments is intercalary and not terminal.

Gametophytes of *L. membranaceum* and *L. mediocre* are heterothallic. Spermatangia and the carpogonial filaments are borne in nemathecia which lie in conceptacles produced by an upgrowth and overarching of the adjoining vegetative tissue. The conceptacles, both male and female, open externally. The orifices of the conceptacles are the minute pin pricks one sees when a thallus is viewed from above with a hand lens.

Every basal cell of a spermatangial nemathecium produces an upright spermatangial filament in which most of the cells cut off two spermatangial mother cells. Several spermatangia are successively developed upon

[1] Howe, 1933; Setchell, 1926, 1929.

[2] Kolderup-Rosenvinge 1909–1924; Kylin, 1928.

each mother cell, and the spermatia liberated from them may accumulate to such an extent that they completely fill the conceptacle (Fig. 181*A*).

The basal cells of female nemathecia send up erect, unbranched filaments. The filaments in the central portion of a nemathecium are three-celled carpogonial filaments in which the terminal cell is the carpogonium. The carpogonium has a long trichogyne that projects through the orifice of the conceptacle (Fig. 181*B*). Filaments toward the periphery of a

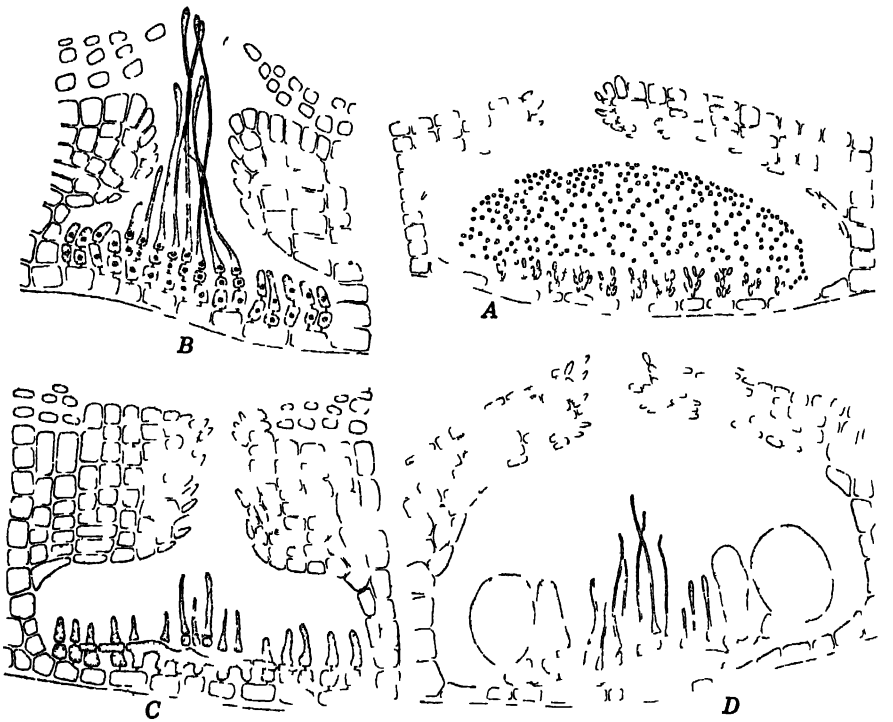


FIG. 181.—*Lithothamnion mediocre* (Foslie) Foslie and Nichols. Semidiagrammatic vertical sections of nemathecia. *A*, spermatangial nemathecium. *B*–*D*, stages in development of cystocarpic nemathecia. *B*, with carpogonial filaments before fertilization. *C*, fusion of ooblast filaments with basal cells of carpogonial and auxiliary cell filaments. *D*, with developing carposporangia. (× 650.)

nemathecium are two-celled auxiliary cell filaments. In the case of *Lithothamnion* the carpogonial and auxiliary cell filaments appear to be homologous structures. The carpogonial and auxiliary cell filaments are so densely crowded in a nemathecium that it is impossible to determine the precise manner in which diploid nuclei reach auxiliary cells at the nemathecial periphery. It is thought[1] that the carpogonium unites with the underlying carpogonial branch cell and that the ooblast grows from this cell to the lower cell (auxiliary cell) of an auxiliary cell filament at the

[1] Kylin, 1928.

nemathecial periphery (Fig. 181*C*). The auxiliary cell filaments and most of the sterile cells of the carpogonial filaments then fuse with one another to form a large disk-shaped *placental cell.* Two- or three-celled gonimoblast filaments grow out from the placental cell margin, and the terminal cell of each gonimoblast filament develops into a large carposporangium (Fig. 181*D*). It is very probable that several of the carpogonia in a nemathecium send out oöblasts to auxiliary cells. Hence the placental cell may be the product of a fusion of a group of carposporophytes instead of a fusion of a single carposporophyte and one or more auxiliary cell filaments.

Fruiting of tetrasporophytes begins with an upgrowth of erect filaments from the lower cells in the distromatic portion. Some of the erect

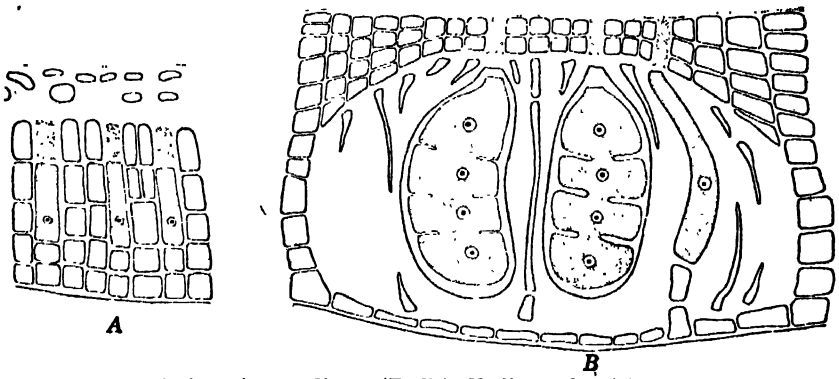


FIG. 182.—*Lithothamnion mediocre* (Foslie) Foslie and Nichols. Development of tetrasporic conceptacles. *A*, shortly after differentiation of tetrasporangia. *B*, with nearly mature tetrasporangia. (× 650.)

filaments in a future fertile area remain sterile. They generally have one dichotomy at the distal end.[1] The fertile filaments are always unbranched. Cessation of upward growth of a fertile filament is followed by a gelatinization of the outermost cell and a conspicuous elongation of the underlying cell, the tetrasporangium (Fig. 182*A*). The tetrasporangium increases greatly in size, and its protoplast divides transversely into four tetraspores. Enlargement of tetrasporangia is accompanied by a disintegration of laterally adjoining portions of the sterile filaments (Fig. 182*B*). There is no disintegration of the outermost portion of the sterile filaments, for they persist and constitute the roof of the cavity (conceptacle) containing the mature tetraspores. Tetrasporic conceptacles differ from those of gametophytes in that they have several minute pore-like openings, each formed by disintegration of a terminal cell of a fertile filament.

[1] Kylin, 1928.

ORDER 4. GIGARTINALES

The Gigartinales are the only tetrasporophytic Florideae in which the auxiliary cell is a vegetative cell of the gametophyte. In some genera the auxiliary cell is the supporting cell of a carpogonial branch; in other genera it lies in vegetative filaments remote from the carpogonial filament. The order includes some 65 genera and 500 species. These have been divided into 20 families.[1]

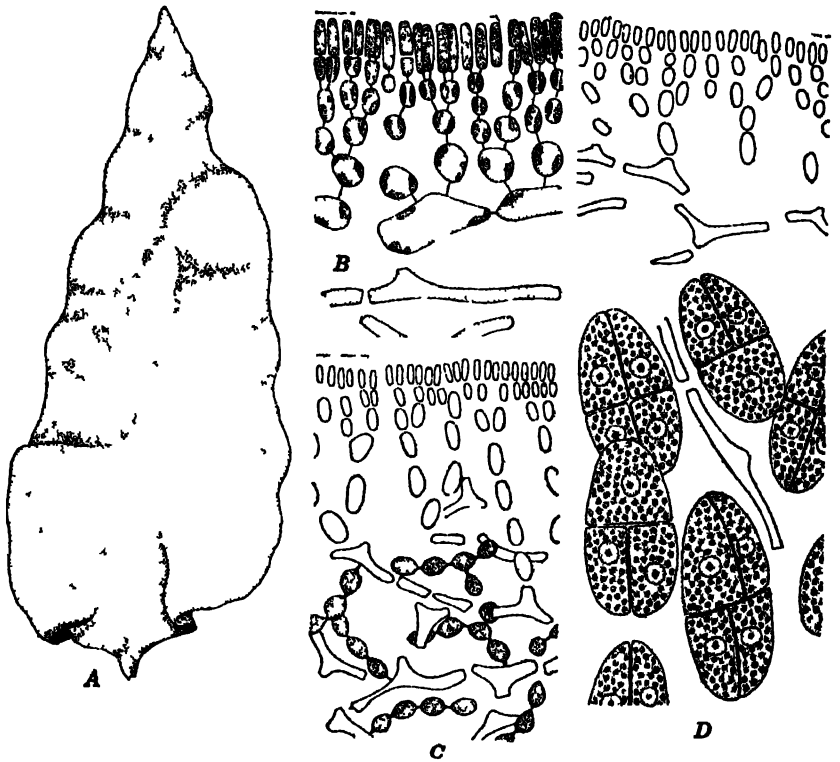


FIG. 183.—*Iridaea cordata* (Turn.) J. G. Ag. *A*, thallus. *B*, vertical section of vegetative portion of thallus. *C–D*, vertical sections of tetrasporophytes with very young and mature tetrasporangia. (*A*, × $\frac{1}{3}$, *B*, *D*, × 650.)

Iridaea is representative of the genera in which the supporting cell of a carpogonial filament is the auxiliary cell. There are 10 to 15 species, and most of them are found only in the Pacific Ocean. *I. cordata* (Turn.) J. G. Ag. is a common alga in the midlittoral zone along the Pacific Coast of this country. It has a more or less discoform holdfast that bears several large, irregularly convoluted, oval blades with acute apices (Fig. 183*A*). Thalli of *I. cordata* are perennial and the overwintering holdfast regenerates new blades each spring. Blades of individuals growing high in the

[1] Kylin, 1932.

sublittoral zone are olive-brown; those of thalli growing near the mean low-tide level are purplish. The generic name is based upon the iridescent sheen of blades when they are submerged.

A blade has a multiaxial growing point. Mature portions of a blade have numerous parallel, colorless, longitudinal filaments at the center and numerous short erect filaments at the exterior (Fig. 183*B*). The erect filaments are compacted into a pseudoparenchymatous tissue containing many chromatophores.

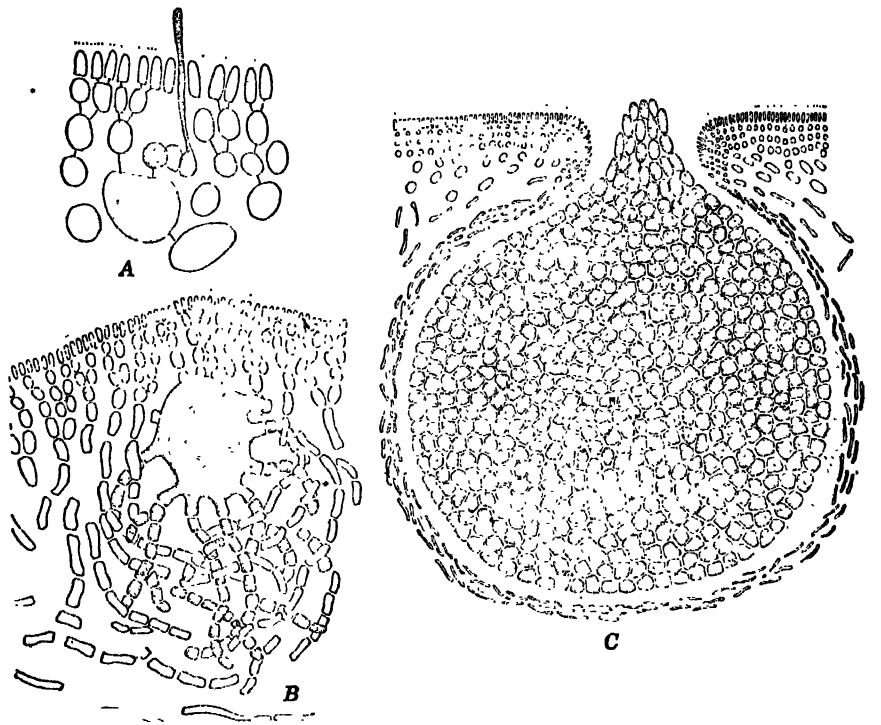


FIG. 184.—*Iridaea cordata* (Turn.) J. G. Ag. *A*, carpogonial filament. *B*, auxiliary cell sending forth gonimoblast filaments. *C*, mass of carposporangia. All figures semidiagrammatic. (*A*, × 650; *B*, × 430; *C*, × 215.)

Gametophytes of *I. cordata* are heterothallic. The male plants produce spermatangia in irregularly shaped sori borne on the flattened sides of blades. The spermatangial mother cells are superficial cells of a thallus, and each of them generally cuts off two spermatangia.[1]

Carpogonial filaments are differentiated near the growing apex of a female gametophyte and are borne upon a large multinucleate supporting cells which lie close to the thallus surface. The carpogonial filament is

[1] Kylin, 1928.

three-celled and so oriented that the carpogonial base adjoins the supporting cell (Fig. 184*A*). Fertilization is followed by an establishment of a short tubular connection between carpogonial base and supporting cell (now the auxiliary cell). Certain other Gigartinales are known[1] to have a migration of the zygote nucleus into the auxiliary cell, and it is very probable that the same is true in *Iridaea*. The auxiliary cell sends forth several gonimoblast filaments that grow toward the thallus interior (Fig. 184*B*). They branch freely, intertwine with one another, and ultimately develop into a massive globose carposporophyte. All food for the early development of a carposporophyte is derived from the auxiliary cell. Later on, vegetative cells adjoining the carposporophyte differentiate into a nurse tissue which furnishes additional food. The gonimoblast filaments of the carposporophyte bear many short lateral branchlets in which each cell develops into a carposporangium. The mature carposporophyte lies deeply embedded within the thallus and is a globose mass of carposporangia (Fig. 184*C*).

The tetrasporophyte develops tetrasporangia internally and in localized patches among the longitudinal axial filaments. An axial filament first sends forth short filaments composed of globose cells densely filled with protoplasm (Fig. 183*C*). Each globose cell of a filament develops into a tetrasporangium whose protoplast becomes quadrately divided into four tetraspores (Fig. 183*D*).

Agardhiella, a genus with three species, is representative of the Gigartinales in which a vegetative cell remote from a carpogonial branch becomes the auxiliary cell. It is a rather common alga of the littoral zone along both the Atlantic and Pacific coasts of this country.

Agardhiella has a cylindrical, branched plant body which is attached to the substratum by a discoid holdfast The erect portion has numerous alternate branches tapering at both base and apex (Fig. 185*A*). The growing points are multiaxial. Mature portions of a branch have a central core of more or less parallel, colorless, longitudinal filaments ensheathed by a layer of erect, dichotomously branched filaments whose cells are progressively smaller from base to apex.

Gametophytes of *Agardhiella* are heterothallic. Male plants produce spermatangia in sori of varying size that are borne upon young branches.[2] A superficial cell of the thallus bears three to five spermatangial mother cells, each of which cuts off two or three spermatangia.

Carpogonial filaments are differentiated less than 1 mm. back from growing tips of female gametophytes. They are borne adaxially upon filaments perpendicular to the central core and generally upon the next to the lowermost cell. The carpogonial filaments are three-celled, and at first grow toward the center of the thallus. As the trichogyne elon-

[1] Kylin, 1923; Sjöstedt, 1926. [2] Kylin, 1928; Osterhout, 1898.

gates, it bends through an arc of 180 degrees, and its distal end grows to the thallus surface (Fig. 185*B*). The carpogonium is always uninucleate; the other two cells of a carpogonial filament contain two to five nuclei each. The auxiliary cell[1] is an intercalary cell midway between base and apex of a vegetative filament perpendicular to the central core. An auxiliary cell is immediately distinguishable from other vegetative cells because of its denser protoplast (Fig. 185*C*). Sometimes it lies in a filament bearing a carpogonial filament, but more often it is in one without carpogonal filaments.

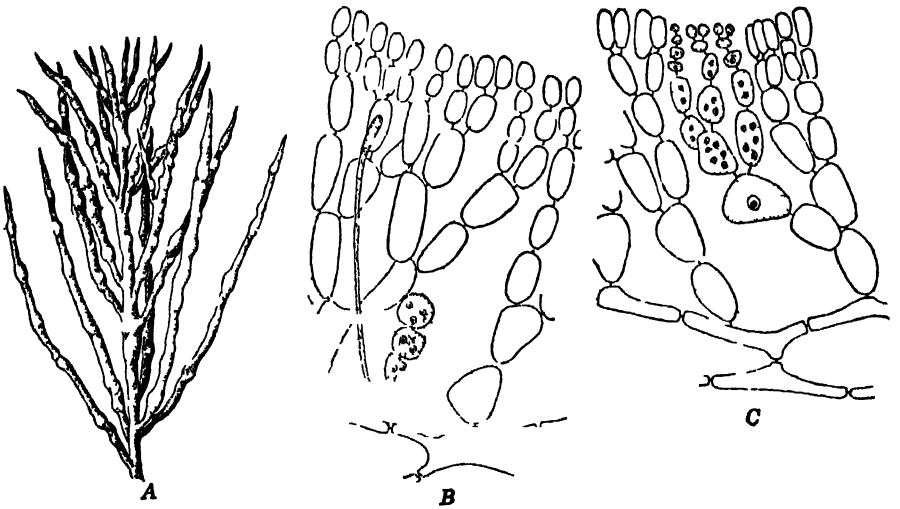


FIG. 185.—*Agardhiella Coulteri* (Harv.) Setchell. *A*, fruiting female gametophyte. *B*, portion of thallus with carpogonial filament. *C*, portion of thallus with auxiliary cell filament. (*A*, × $\frac{1}{2}$; *B–C*, × 430.)

Fertilization is followed by an outgrowth of a long delicate tube, the ooblast, from the carpogonial base to an auxiliary cell.[1] The zygote nucleus then migrates through the ooblast into the auxiliary cell. There is a considerable delay between entrance of the zygote nucleus and production of the first gonimoblast filament from the auxiliary cell. During this time, adjoining vegetative cells send out tubular processes that cut off small cells densely filled with protoplasm (Fig. 186*A*). These cells develop into a nurse tissue surrounding the developing carposporophyte. Differentiation of the nurse tissue is accompanied by an upgrowth of overlying tissue to form the opening, ostiole, through which the carpospores eventually escape. The gonimoblast initial cut off from an auxiliary cell develops into a radiately branched spherical mass of intertwined gonimoblast filaments (Fig. 186*B*). Most of the filaments lie internal to the nurse tissue, but some of them are haustorial

[1] Kylin, 1928; Osterhout, 1898.

in nature and penetrate the nurse tissue. Carposporangia are developed from terminal cells of branch tips at the periphery of a carposporophyte. Carpospores liberated from the carposporangia float out through the ostiole.

Agardhiella is one of the genera in which there is some cultural evidence[1] that carpospores develop into tetrasporophytes, hence clear

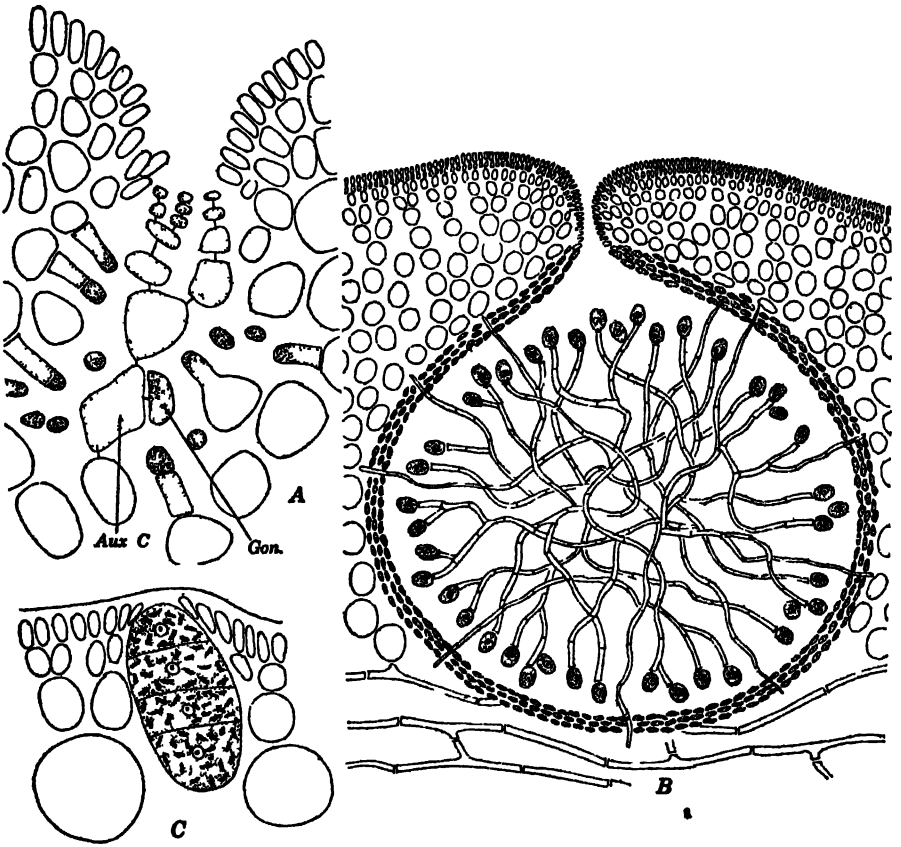


FIG 186 —*Agardhiella Coulteri* (Harv) Setchell *A*, portion of a female gametophyte containing an auxiliary cell (*Aux C*) that has formed the first cell (*Gon*) of a gonimoblast filament *B*, diagrammatic vertical section of a carposporophyte with young carposporangia. *C*, tetrasporangium (*A*, × 430, *B*, × 80, *C*, × 325)

evidence that tetraspores give rise to sexual plants. Tetrasporangia are differentiated from superficial cells of a tetrasporophyte (Fig 186*C*). Development of tetrasporangia is accompanied by an upgrowth of adjoining vegetative tissues. Thus the mature tetrasporangia lie embedded a short distance beneath the thallus surface At the time of spore formation the protoplast divides transversely into four tetraspores.

[1] Lewis, 1912

ORDER 5. RHODYMENIALES

The Rhodymenialcs are tetrasporophytic Florideae in which the auxiliary cell is a special cell differentiated before fertilization. It is the terminal member of a two-celled filament borne upon the supporting cell of a carpogonial filament. Several genera have the supporting cell producing two filaments, each of which terminates in an auxiliary cell. The order includes about 25 genera and 130 species.[1] These are placed in two families.[2]

Gastroclonium has three species, one of which, *G. Coulteri* (Harv.) Kylin, is found along the west coast of the United States. The best-known species, *G. ovale* (Huds.) Kutz. [often called *Lomentaria ovalis*

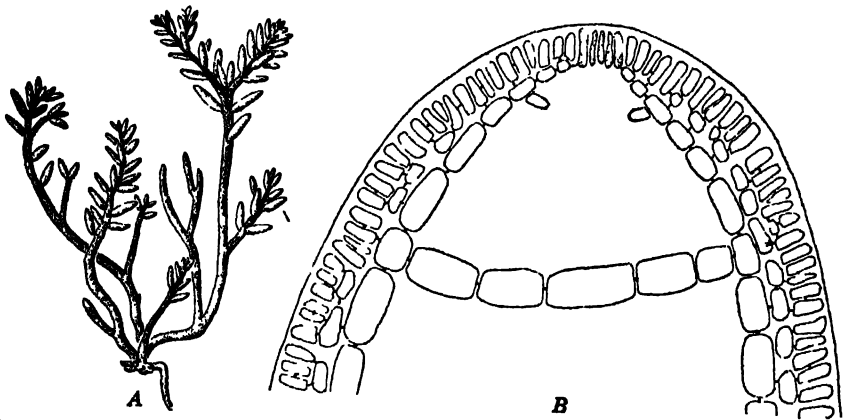


FIG. 187.—*Gastroclonium Coulteri* (Harv.) Kylin. *A*, thallus. *B*, diagrammatic vertical section of a thallus apex. (*A*, × ½, *B*, × 215.)

(Huds.) J.Ag. or *Chylocladia ovalis* (Huds.) Harv.], is European. *Gastroclonium* is a perennial alga with an erect cylindrical thallus that is irregularly or dichotomously branched and with the branch apices broadly rounded (Fig. 187*A*). The lower portions of a thallus are solid; the upper portions are hollow and transversely divided into barrel-shaped cavities by septa one cell in thickness.

A branch apex has a ring of about 15 apical cells.[3] The longitudinal axial filaments, cut off posterior to the apical initials, lie in a hollow cylinder instead of in a solid cylinder as in most other multiaxial Florideae. Each cell of an axial filament bears a short, compact, lateral filament upon its external face. They are outwardly branched and compacted into the pseudoparenchymatous tissue which surrounds the central cavity of mature portions of a thallus (Fig. 187*B*). Septation of the central cavity is due to a development of horizontal unbranched fila-

[1] Kylin, 1931*A*. [2] Bliding, 1928; Kylin, 1931*A*. [3] Bliding, 1928.

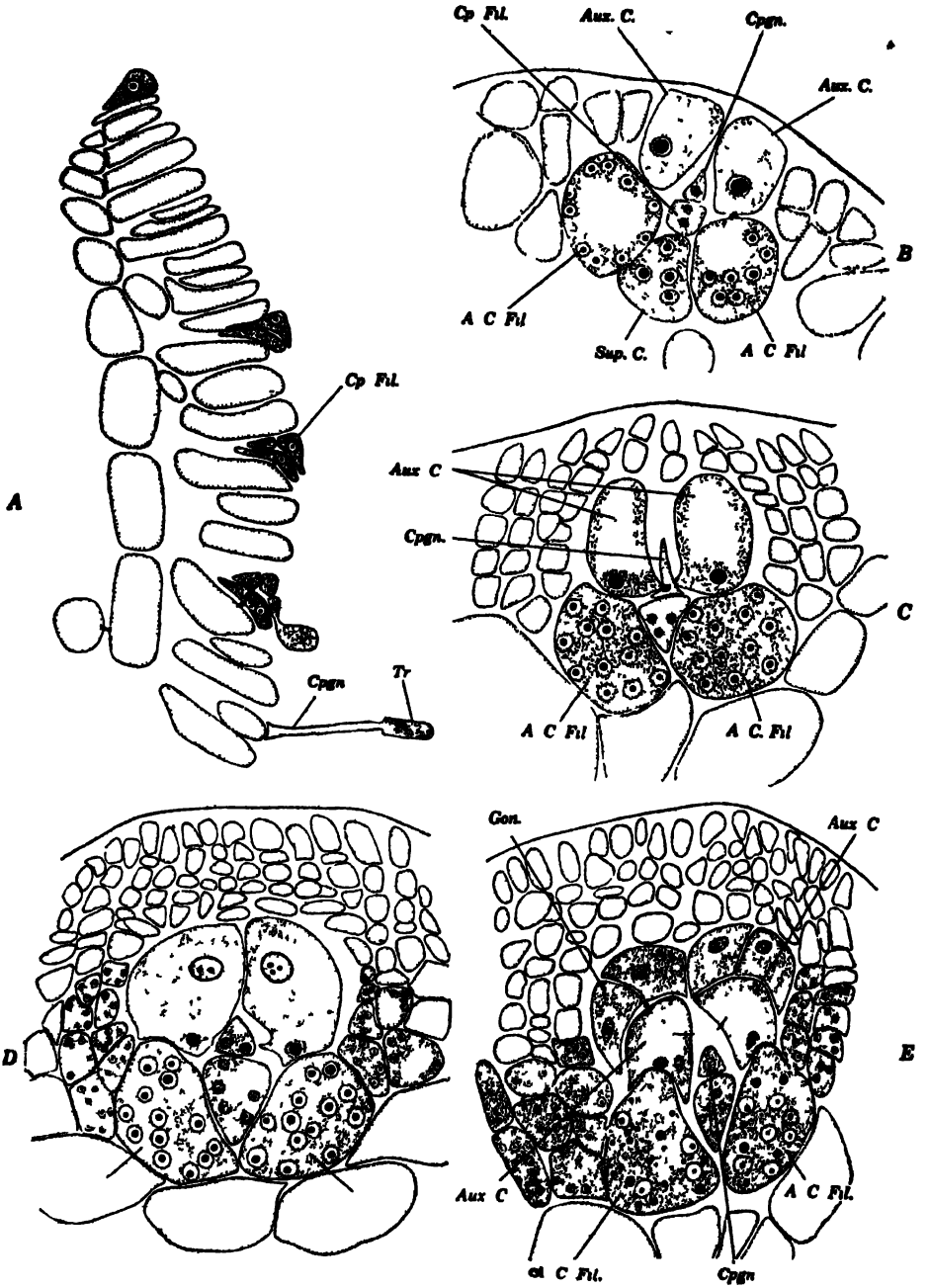


FIG 188.—*Gastroclonium ovale* (Huds.) Kütz. *A*, vertical section of a thallus apex with young carpogonial filaments. *B*, transverse section of a carpogonial filament and the adjacent auxiliary cell filaments before fertilisation. *C*, the same after fusion of the carpogonial base with the auxiliary cells. *D*, the same after migration of a diploid nucleus into each auxiliary cell. *E* after the auxiliary cells have cut off initials of gonimoblast filaments. (*After Blidding*, 1928.) (*Aux C*, auxiliary cell; *A C. Fil.*, auxiliary cell filament; *Cpgn*, carpogonium; *Cp Fil*, carpogonial filament, *Gon* gonimoblast, *Sup C*, supporting cell, *Tr*, trichogyne.) (*A–B*, × 500, *C–E* × 400.)

ments on the internal face of axial filaments. They are formed simultaneously at the same level upon all axial filaments, and they grow inward until they meet one another at the center of the thallus.

Gametophytes of *Gastroclonium* are heterothallic, but male plants are much scarcer than female ones.[1] The spermatangia lie in irregularly shaped sori borne upon the bladder-like branchlets at the distal end of a thallus. The spermatangial mother cells are borne at tips of lateral filaments from the axial filaments. Each spermatangial mother cell generally bears three spermatangia.[1]

The supporting cell of a carpogonial filament is differentiated very close to the thallus apex, and it is borne directly upon a cell of an axial filament. The supporting cell gives rise to a four-celled carpogonial

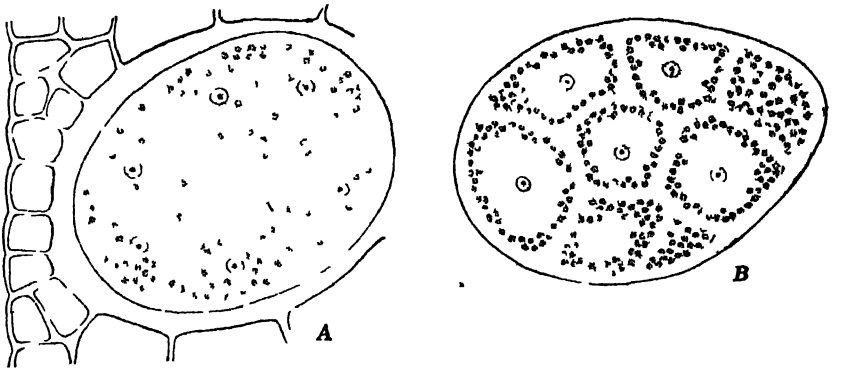


FIG 189.—*Gastroclonium Coulteri* (Harv.) Kylin. *A*, young parasporangium. *B*, parasporangium with mature paraspores. (× 325.)

filament in which the lowermost cell is binucleate and the other cells are uninucleate.[2] A mature carpogonial filament is so curved that the carpogonial base adjoins the lowermost cell of the filament (Fig. 188*A*). The supporting cell also produces two auxiliary cell filaments, one on either side of the carpogonial filament. These filaments are developed before fertilization. Each of them has a large multinucleate basal cell and a small uninucleate distal cell—the auxiliary cell (Fig. 188*B*). After fertilization each auxiliary cell sends out a short basal protuberance that grows to and fuses with the carpogonial base (Fig. 188*C*). A diploid daughter nucleus of the zygote nucleus migrates[2] into each of the two auxiliary cells (Fig. 188*D*). Each auxiliary cell then cuts off a succession of gonimoblast filament initials at the outer face (Fig. 188*E*). Cells cut off from the gonimoblast filament initials develop directly into carposporangia, each containing a single diploid nucleus. During the course of carposporangial development, the gonimoblast filament initials,

[1] Grubb, 1925. [2] Bliding, 1928.

the auxiliary cell filaments, the supporting cell, and certain of the adjoining vegetative cells fuse with one another to form a large multinucleate, bilobed, placental cell which furnishes food for the development of carposporangia. At the same time vegetative tissues lateral to the carposporophyte and placental cell grow upward into a closed pericarp without an ostiole.

Tetrasporangia are formed upon the ultimate branchlets of a tetrasporophytic thallus. They are differentiated from terminal cells of the lateral filaments at the exterior face of axial filaments. Developing tetrasporangia have a tetrahedral division of their protoplasts into four tetraspores.[1] The tetrasporangia lie embedded just within the thallus surface. Tetrasporophytes of *G. Coulteri* may also form parasporangia. A developing parasporangium contains 15 to 20 nuclei. Later on there is an inward furrowing of the plasma membrane (Fig. 189*A*) that divides the sporangial contents into 15 to 20 uninucleate protoplasts, each of which is a paraspore (Fig. 189*B*).

ORDER 6. CERAMIALES

The Ceramiales are the only tetrasporophytic Florideae in which the auxiliary cell is formed subsequent to fertilization. The auxiliary cell is always borne directly upon the supporting cell of a carpogonial filament. The order includes about 160 genera and 900 species. These are divided into three families.[2]

Polysiphonia is one of the few genera in which there has been a demonstration[3] that carpospores grow into tetrasporophytes and that tetraspores grow into gametophytes. The nuclear behavior[4] throughout the entire life cycle is also definitely known.[5] *Polysiphonia* is a very common alga along the Atlantic Coast of this country, and several species grow in abundance upon Fucaceae of the upper littoral zone. The genus is less abundant along the Pacific Coast, where it is found chiefly in the lower littoral and sublittoral zones.

Germinating tetraspores and carpospores of *Polysiphonia* divide transversely into a small lower cell and a large upper cell, both of which also divide transversely.[6] The lowermost of the four cells develops into an elongate unseptate rhizoid whose distal end expands into an irregularly lobed attachment disk. The uppermost cell becomes an apical cell

[1] Bliding, 1928. [2] Schmitz and Hauptfleisch, 1896–1897.

[3] Lewis, 1912, 1914. [4] Yamanouchi, 1906.

[5] The cultural investigations of Lewis and cytological work of Yamanouchi were upon a species collected at Woods Hole, Massachusetts. They called this species *P. violacea* (Roth) Grev. Professor W. R. Taylor informs me that *P. violacea* is found only in European waters and that the American species given this name is *P. flexicaulis* Harv.

[6] Derick, 1899; Kylin, 1917*A*.

that cuts off a linear file of axial cells at its posterior face. Cell division in a vertical plane begins when the plantlet is six or seven cells in length, and each axial cell in the basal portion of the file cuts off an encircling layer of *pericentral cells* (Fig. 190*A*). The number of encircling pericentral cells is fairly constant for any given species and ranges from 4 to 24. Many of the first-formed pericentral cells send out secondary rhizoids which help anchor the thallus Each axial cell two or three removed from the apical cell may divide diagonally at the upper end and

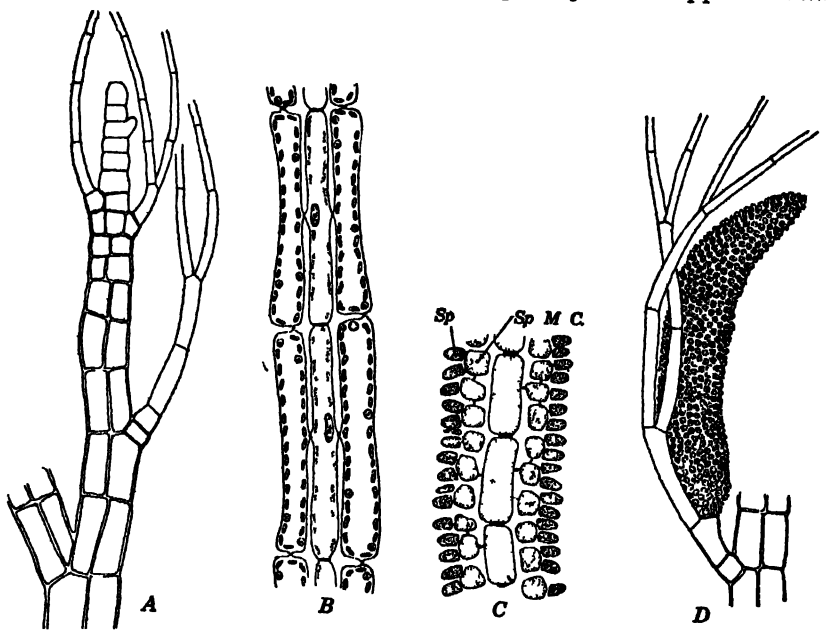


FIG 190.—*A–B, Polysiphonia flexicaulis* Harv *A*, surface view of growing apex. *B*, vertical section of mature region *C D, Polysiphonia* sp *C*, optical section of a fertile trichoblast with spermatangial mother cells (*Sp M C*) bearing spermatangia (*Sp*) *D*, surface view of a fertile spermatangial trichoblast (*A*, × 430, *B–C*, × 650, *D*, × 325)

cut off a small *trichoblast initial.* Repeated division of the trichoblast initial produces a uniseriate dichotomously forked gradually tapering multicellular filament—the *trichoblast.* Cells of a trichoblast are uninucleate and colorless or with very faintly colored chromatophores. The trichoblasts are generally borne in a spiral succession along the thallus. Some species have an early abscission of the trichoblast; other species retain all or certain of them for a considerable time. The cells of the axial filament cut off an encircling layer of pericentral cells after they have cut off the trichoblast initial. Each cell of the transverse tier thus formed elongates to several times its original length (Fig. 190*B*). Mature portions of thalli of most species retain this "polysiphonous" organization, but there are certain species in which older portions of the

thallus may also become "corticated" through the formation of a layer of small cells external to the pericentral cells.

Lateral branches are generally differentiated close to the growing apex and before the formation of pericentral cells. An initial of a lateral branch is formed in the same manner as that of a trichoblast. In some cases, as in *P. nigrescens* (J. E. Smith) Grev., they develop axillary to and from the basal cell of a trichoblast.[1] In other cases they replace certain trichoblasts, and sometimes there is a development of branches upon mature portions of a thallus.

Gametophytes of most, if not all, species of *Polysiphonia* are heterothallic.[2] The spermatangia are produced upon fertile trichoblasts borne near the thallus apex. A developing, fertile trichoblast branches dichotomously after it has become two or three cells in length. Both arms of the dichotomy may develop into a fertile axis [*P. lanosa* (L.) Tandy[2]], but in most species[3] one arm develops into a short fertile axis and the other into a long, repeatedly branched, sterile axis (Fig. 190*D*). A fertile axis is several cells in length and unbranched. The two lowermost cells are sterile; the others each cut off a variable number of encircling pericentral cells. Each pericentral cell cuts off one or more spermatangial mother cells at the free face.[3] According to the species,[2] the spermatangial mother cell bears two, three, or four spermatangia (Fig. 190*C*). The spermatium is liberated by a rupture of the spermatangial wall, and, after it has been discharged, there may be a proliferation of a new spermatangium within the old empty spermatangial wall.

The carpogonial filament and associated structures are borne upon a greatly reduced, fertile trichoblast of a female gametophyte. The initial cell of a fertile female trichoblast is cut off from an axial filament cell three or four cells back from the thallus apex. The axial filament cell also cuts off an encircling ring of pericentral cells about the same time it cuts off the trichoblast initial. The trichoblast initial looks so much like one of the pericentral cells that it is often called the *fertile pericentral cell.*

The trichoblast initial grows into a trichoblast five to seven cells in length, and one in which the two lowermost cells each cut off an enshcathing layer of pericentral cells (Fig. 191*A*). One of the adaxial cells in the upper tier of pericentral cells is the supporting cell of the future carpogonial filament. This supporting cell cuts off an initial at its free face, and this initial produces a curved, four-celled, carpogonial filament in which the terminal cell metamorphoses into a carpogonium with a long erect trichogyne (Fig. 191*B–C*). Development of the carpogonial filament is accompanied by a cutting off of two *sterile*

[1] Kolderup-Rosenvinge, 1909–1924. [2] Grubb, 1925.
[3] Grubb, 1925; Kylin, 1923.

filament initials from the supporting cell. One initial is cut off basally, the other laterally. The basal sterile filament initial remains undivided for a time; the lateral one divides[1] immediately (Fig. 191*D–E*).

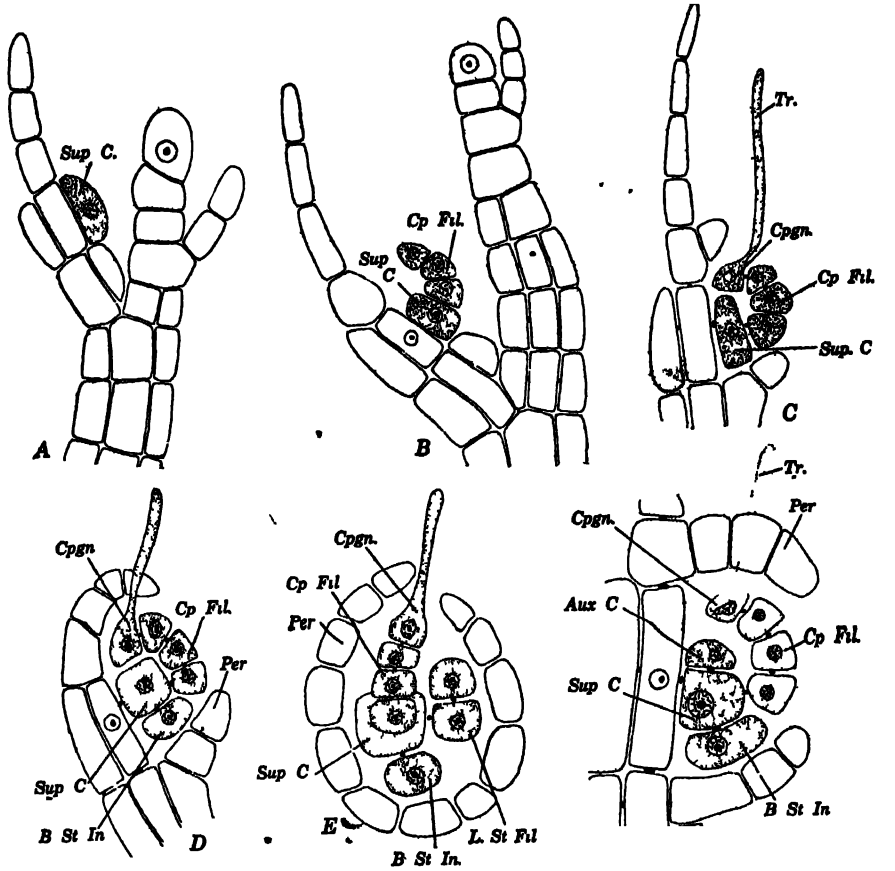


FIG. 191.—*Polysiphonia flexicaulis* Harv. *A–E*, longitudinal sections showing the development of female reproductive structures up to the time of fertilization. *A*, before development of carpogonial filament. *B–C*, developing and mature carpogonial filaments. *D*, after cutting off of sterile filament initials. *E* tangential section of Fig. *D*, showing the basal and lateral sterile filaments. *F*, after fertilization and formation of the auxiliary cell. (*Aux C*, auxiliary cell, *B St In*, basal sterile initial, *Cpgn*, carpogonium, *Cp Fil*, carpogonial filament, *L St Fil*, lateral sterile filament, *Per*, pericarp, *Sup C.*, supporting cell, *Tr*, trichogyne.) (× 875.)

Fertilization takes place at this stage of development and is effected in the usual manner.[2] Shortly afterward the lateral sterile filament becomes 4- to 10-celled, and the basal sterile initial develops into a 2-celled filament. Following this the supporting cell buds off a daughter cell at the upper side (Fig. 191*F*). This cell (the auxiliary cell) lies below, and soon establishes a tubular connection with, the carpogonial

[1] Kylin, 1923. [2] Yamanouchi, 1906.

base. A diploid daughter nucleus of the zygote nucleus next migrates into the auxiliary cell. The gonimoblast grows from the upper side of the auxiliary cell (Fig. 192*A*) It consists of a densely compacted mass of gonimoblast filaments in which each cell is uninucleate and has a diploid nucleus The carposporangia are elongate and are developed only from terminal cells of gonimoblast filaments. The single carpospore

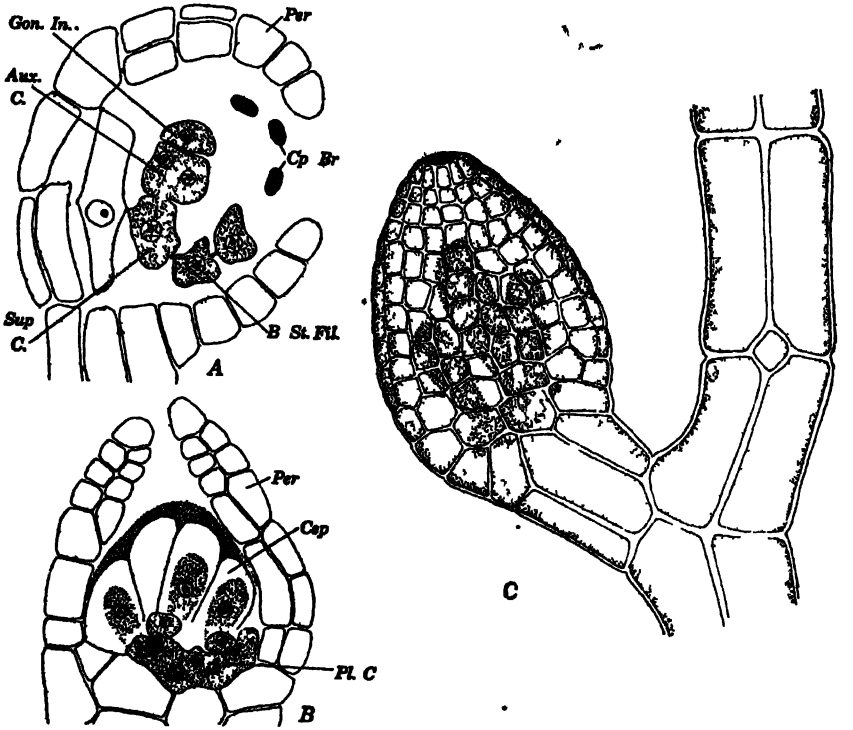


FIG 192.—*A–B, Polysiphonia flexicaulis* Harv *A*, after formation of first gonimoblast initial *B*, carposporophyte with young carposporangia *C*, surface view of mature pericarp of an unknown species of *Polysiphonia* (*Aux C* auxiliary cells *B St Fil*, basal sterile filament, *Cp Br*, remains of carpogonial filament, *Csp* carposporangium *Gon In*, gonimoblast initial, *Per*, pericarp, *Pl C*, placental cell, *Sup C*, supporting cell (*A*, × 875, *B*, × 430, *C*, × 215)

within each carposporangium has a diploid nucleus Development of the carposporophyte is accompanied by a gradual fusion of the supporting cell, the auxiliary cell, and cells of the sterile filaments into a single large, irregularly shaped, placental cell (Fig. 192*B*) The carpogonial filament withers and does not contribute to the placental cell[1] The mature carposporophyte is surrounded by a large urn-shaped pericarp with a conspicuous ostiole at the distal end (Fig 192*C*). Development of the pericarp begins before fertilization, and it is developed from pericentral trichoblast cells adjacent to the supporting cell.

[1] Yamanouchi, 1906

Carpospores liberated from the carposporangia develop into tetrasporophytes.[1] Only one pericentral cell of any transverse tier in a fruiting tetrasporophyte produces a tetrasporangium. However, tetrasporangia are usually developed in several successive tiers. The fertile pericentral cell of a tier is smaller than the other pericentral cells. It first cuts off a daughter cell at its outer face. In some species, as *P.*

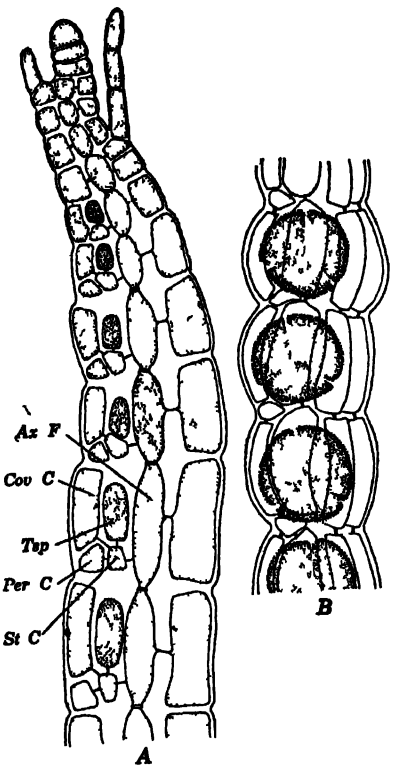


FIG. 193.—*Polysiphonia* sp. *A*, optical section of apex of tetrasporophyte with young tetrasporangia. *B*, surface view of older portion containing mature tetraspores. (*Ax F.*, axial filament, *Cov C*, cover cell, *Per C*, peripheral cell, *St C*, stalk cell, *Tsp*, tetrasporangium.) (*A*, × 650, *B*, × 215.)

nigrescens, the daughter cell cuts off two *cover cells* at the upper face;[2] in other species, as *P. violacea* (Roth) Grev.,[3] the daughter cell cuts off two large cover cells and a small *peripheral cell* (Fig. 193*A*). In either case the fertile pericentral cell then divides transversely. The lower daughter cell is a stalk cell, the upper is the tetrasporangium. The sporangial cell increases to several times its original size; its single nucleus divides meiotically,[4] and the protoplast divides to form four tetrahedrally disposed tetraspores (Fig. 193*B*). The tetraspores are

[1] Lewis, 1912, 1914. [2] Kolderup-Rosenvinge, 1909–1924; Kylin, 1923.
[3] Kolderup-Rosenvinge, 1904–1924. [4] Yamanouchi, 1906.

liberated by a rupture of the sporangial wall and a longitudinal spreading apart of the two elongate cover cells. They develop into gametophytes.[1]

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[1] Lewis, 1912, 1914.

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CHAPTER IX

MYXOTHALLOPHYTA

The Myxothallophyta or slime molds resemble the true fungi in their lack of photosynthetic pigments and their food reserves. They differ from fungi in that the plant body is a naked amoeboid mass of protoplasm throughout all stages of vegetative development. The vegetative body may be a single large multinucleate protoplast, a *plasmodium;* or a *pseudoplasmodium* that results from an aggregation of many small uninucleate protoplasts that retain their individuality. Reproduction of Myxothallophyta is by a formation of many small uninucleate spores, each with a distinct spore wall. In a majority of genera the spores are borne within or upon a fructification of definite form. In a few genera there is a production of an amorphous mass of spores. According to the genus, germinating spores give rise to naked uniflagellate swarm spores or to naked nonflagellate amoeboid cells (*myxamoebae*). The evidence thus far accumulated seems to show that these bodies are gametic in nature and that they unite in pairs to form an amoeboid zygote in which there is soon a union of the two gamete nuclei. The zygote nucleus may divide and redivide equationally, thus producing a plasmodium. Sometimes the zygote nucleus remains undivided, and many zygotes become apposed to one another in a pseudoplasmodium. The last series of nuclear divisions in plasmodial development may be reductional, or they may be equational. In the latter case meiosis takes place in the spores.

The systematic position of the slime molds is a matter of dispute. Some botanists hold that they show so many affinities with the Protozoa that they should be excluded from the plant kingdom. A much larger number hold that the slime molds are more plant-like than animal-like in nature and should be included in the plant kingdom. Most of those including slime molds among plants place them in a division (variously called *Myxothallophyta,*[1] *Mycetozoa, Myxophyta*) equal in rank to the fungi instead of placing them among the various classes of fungi. All botanists recognizing the Myxothallophyta as a distinct division agree that the true slime molds (the Myxomycetae) belong in the division. There is disagreement as to whether certain other organisms with much the same structure should be placed alongside the Myxomycetae.

[1] Schröter, 1889.

Several[1] think that the Phytomyxinae (Plasmodiophoraceae) are more closely related to the chytridiaceous Phycomycetae than they are to Myxomycetae. Others[2] exclude from the plant kingdom the slime molds with a pseudoplasmodium (the Acrasieae).

The three classes here included in the Myxothallophyta are:

Myxomycetae in which the vegetative body is a free-living plasmodium that develops into a fructification of definite form. The spores may be borne within or externally upon the fructification.

Phytomyxinae in which the vegetative body is a parasitic plasmodium developing within tissues of angiosperms. At the time of reproduction the plasmodium breaks up into a mass of spores that are usually without definite arrangement.

Acrasieae in which there is a pseudoplasmodium whose individual myxamoebae combine to form a fructification of definite form.

These three classes seem to have sufficient in common to warrant their inclusion in the same division. They appear to have been derived from protozoa. This derivation may have been monophyletic or, as has recently been suggested,[3] along three independent lines. If the latter hypothesis is correct, the Myxothallophyta are an artificial and not a natural group. The Labyrinthuleae are sometimes included as a fourth class of the Myxothallophyta, but these organisms are so imperfectly known that their real relationships are uncertain.

CLASS 1. MYXOMYCETAE

The vegetative bodies of Myxomycetae are naked, amoeboid, multinucleate, free-living *plasmodia* that may be several centimeters in diameter. A plasmodium lacks photosynthetic pigments, and it obtains food by ingesting microscopic organisms, spores, or small particles of dead plant or animal tissues. At the time of reproduction a plasmodium heaps up to form one or more sessile or stalked sporangia. There is generally a wall-like layer (the *peridium*) at the outside of each sporangium, and it is derived from waste materials excreted by the protoplasm. The protoplast of a sporangium becomes divided into a large number of small spores, each surrounded by a definite wall. A germinating spore produces one to four uniflagellate swarmers. There may be an immediate union of the swarmers in pairs, or they may multiply vegetatively for one or more generations before a fusion in pairs takes place. Union of a pair of gametes is soon followed by a union of the two gamete nuclei. The resultant zygote is amoeboid, and it grows directly into a multinucleate plasmodium by repeated equational division of the fusion nucleus. There are about 50 genera and 400 species of myxomycetes.

[1] Fitzpatrick, 1930; Gäumann and Dodge, 1928; Martin, 1932.
[2] Jahn, 1928*A*. [3] Cook, 1933.

The Myxomycetae are divided into the two following subclasses:

Endosporeae in which the spores are borne internally within a sporangium

Exosporeae in which the spores are borne externally and in considerable numbers on an erect branching fruiting pillar.

SUBCLASS 1. ENDOSPOREAE

The myxomycetes in which spores are formed within a sporangium, the Endosporeae, include all but one genus of the Myxomycetae. All genera of the Endosporeae have a well-developed plasmodium. These



FIG. 194.—Plasmodium of *Didymium* sp. (× 30)

plasmodia are generally found creeping over moist decaying matter. Favorable substrata include rotting logs, old wood piles, and decaying leaves. Plasmodia are also an important constituent of the microflora of the soil,[1] but ordinarily their presence in soil can only be demonstrated by isolation in culture.

The cytoplasm of a plasmodium is differentiated into an inner granular portion, which contains the nuclei, and an outer enucleate portion. Increase in size of a plasmodium is accompanied by an increase in number of nuclei by mitotic division.[2] All nuclei of a plasmodium divide at approximately the same time, but this may take place at any hour, day or night.[3] A developing plasmodium creeps slowly over the substratum

[1] Thom and Raper, 1930

[2] Harper, 1900; Schunemann, 1930; Howard, 1932; Jahn, 1911.

[3] Howard, 1932

in a more or less amoeboid fashion. The protoplasm at the advancing margin is an irregularly lobed mass; posterior to this the protoplasm tends to lie in a fan-shaped reticulum with numerous irregularly shaped anastomoses (Fig. 194). Growth continues as long as food and moisture are abundant, and plasmodia have continued vegetative growth on synthetic media for more than a year.[1] Sometimes a developing plasmodium fragments into two or more portions. These fragments may continue growth as independent organisms, or they may reunite with one another to form a single organism Two adult plasmodia of independent origin

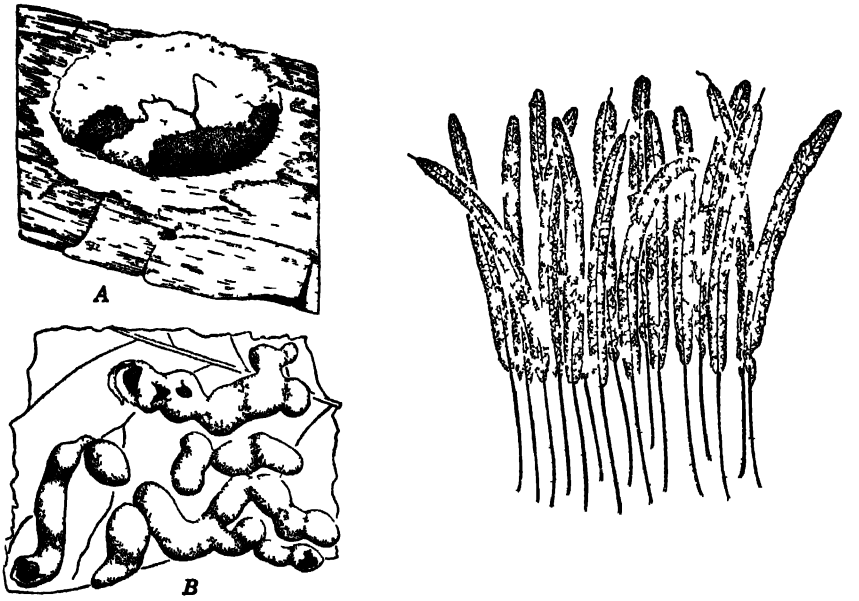


FIG 195.—Fruiting bodies of Myxomycetae *A Fuligo septica* (L.) Web *B, Physarum alpinum* G List *C, Stemonitis splendens* Rost (*A* × ¼ *B*, × 10, *C*, × 5)

may also coalesce, but this only takes place when the two are of the same species.

If conditions of moisture, temperature, or food supply become unfavorable, a plasmodium may become concentrated into one or more thick, horny resting stages (*sclerotia*) that may revert to the plasmodial condition with a return of favorable conditions Most sclerotia more than a year old have lost the capacity to revert, but in exceptional cases they have been reactivated after storage for more than five years.

A plasmodium generally migrates to a more brightly illuminated and drier side of the substratum just before it fruits According to the species, it produces a single sporangium or a number of sporangia. If all or the major portion of a plasmodium develops into a single flattened,

[1] Howard, 1931*A*

biscuit-shaped sporangium, the fructification is an *aethalium* (Fig. 195*A*). If the single fructification retains more or less of the reticulate outline of the plasmodium, it is known as a *plasmodiocarp* (Fig. 195*B*). In most species there is a formation of several sporangia. Here there is a fragmentation of the plasmodium just prior to or during the early stages of sporangial development. Since the various fragments migrate but little, the sporangia developed from them tend to lie in a cluster (Fig 195*C*). Certain species have an immediate excretion of a protective layer of waste material, the sporangial wall or *peridium*, after a rounding up of a protoplasmic fragment In other species peridium formation is preceded by an excretion of a column of waste material that elevates the proto-

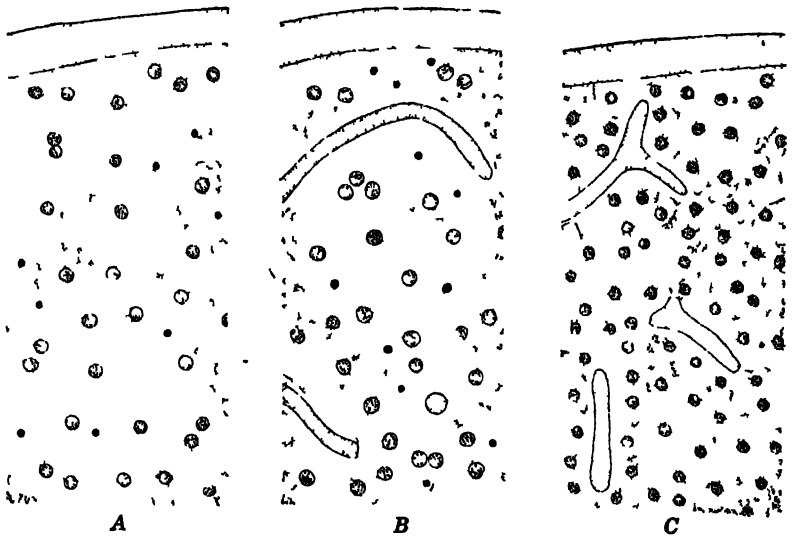


FIG 196 *Physarum* sp , development of sporangium *A*, before formation of capillitium *B*, after formation of capillitium *C*, cleavage into spores (× 430)

plasmic mass above the substratum. This results in a stalked sporangium. In either case there may be a discarded remnant of the plasmodium, the *hypothallus*, at the base of the sessile or stalked sporangia.

The protoplasm of a sporangium is multinucleate and with the nuclei uniformly distributed throughout the cytoplasm (Fig. 196*A*). Sooner or later, after differentiation of the peridium, there is an appearance of furrows at various points in the plasma membrane of the cytoplasm. They become deeper, branch and rebranch, and finally cut the protoplasm into small uninucleate protoplasts [1] Each uninucleate protoplast formed by this progressive cleavage then rounds up, secretes a wall, and becomes a spore. Progressive cleavage of the multinucleate protoplasm within a sporangium is frequently preceded by the develop-

[1] Harper, 1900, 1914; Howard, 1931.

ment of numerous branched or unbranched canals in which excreted materials are deposited.[1] The threads of waste material thus cast in molds of living protoplasm persist after spore formation and constitute the *capillitium* that lies intermingled with spores within a sporangium (Fig. 196*B–C*). The peridium cracks open or flakes away after the spores are mature. Sifting out of spores from an opened sporangium is gradual if they lie entangled among capillitial threads.

Spore germination (Fig. 197*A–C*) may take place immediately after liberation. On the other hand, it may be long delayed if conditions are unfavorable, and spores of certain species[2] may remain viable for more than 25 years. Spores of some species regularly produce a single uni-

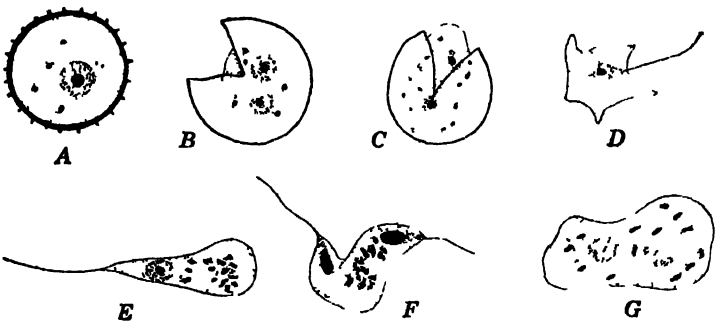


FIG. 197 Spore germination of *Physarum polycephalum* Schw. *A*, spore *B C*, germination. *D E*, gametes *F*, gametic union *G*, germination of zygote (*After Howard*, 1931.) (× 1,200)

flagellate swarmer; those of other species regularly produce two or four swarmers.[3] According to the species there is either a rupture of the spore wall at the time of germination or a development of a pore in the wall.[4] The protoplast within the wall may develop into a uniflagellate swarmer before emerging,[5] but in most cases it emerges in an amoeboid fashion and develops a flagellum after emergence. If the protoplast is one that divides to form two or four daughter protoplasts that become swarmers, the division may take place prior to[4] or after[6] emergence. In many cases the uniflagellate swarmers are gametes that unite with each other in pairs (Fig. 197*E G*). More rarely[7] the swarmers give rise to one or more successive generations of uniflagellate swarmers before gametic union takes place. If environmental conditions become unfavorable, a swarmer may lose its flagellum, assume a spherical shape, and secrete a thin wall.[8] Such spore-like bodies germinate to form a single swarmer upon a return of favorable conditions.

[1] Harper and Dodge, 1914; Howard, 1931. [2] Smith, E. C., 1929*A*.
[3] Smith, E. C., 1929 [4] Gilbert, F. A., 1928 [5] Jahn, 1928.
[6] Jahn, 1904; Howard, 1931; Gilbert, F. A., 1928.
[7] Wilson and Cadman, 1928. [8] Howard, 1931.

Fusion in pairs generally takes place while the gametes are actively motile and by an apposition of their posterior poles,[1] but it may take place after the gametes have lost their flagella and have become amoeboid.[2] Union of a pair of gametes is soon followed by a fusion of the two gamete nuclei. The fusion nucleus divides and redivides equationally as the amoeboid zygote develops into a plasmodium. In rare cases one or more amoeboid gametes may unite with a young zygote before fusion of the two haploid nuclei.[3] These embryonic plasmodia may or may not unite with others containing two or more haploid nuclei. Embryonic plasmodia with several haploid nuclei soon have a fusion of them in pairs to form diploid nuclei.

There is an equational division of the diploid nuclei throughout the entire vegetative development of a plasmodium. Meiosis takes place at some stage before the production of gametes, but the exact stage at which it occurs is still uncertain. In a few species[4] there is good evidence that it occurs in developing sporangia just before progressive cleavage. It has also been stated[5] that the nucleus in a spore is diploid and that it divides meiotically into four daughter nuclei, three of which degenerate. Unfortunately, a detailed account of meiosis in spores of this type has never been published.

The classification of the Endosporeae is based upon the structure of the mature fruiting body. Upon this basis the subclass has been divided[6] into four orders that differ from one another in calcareous or noncalcareous nature of the peridium, the presence or absence of a true capillitium, and the color of the spores.

SUBCLASS 2. EXOSPOREAE

The Exosporeae have the "spores" borne externally and in considerable numbers on an erect branching fruiting pillar. There is but one genus (*Ceratiomyxa*) with four closely related species.

The entire vegetative development of a plasmodium of *Ceratiomyxa* takes place within old rotten logs, and it does not migrate to the surface of the log until the time of fruiting. Minute papillate masses of protoplasm then appear on the surface of the dead wood within which the plasmodium has completed its vegetative development. Each papilla becomes differentiated into a central gelatinous core of nonliving material (the *sporophore*) and an ensheathing layer of protoplasm (Fig. 198). The sporophore is thought to be homologous with the hypothallus of Endosporeae rather than homologous with their sporangia.[7] As the sporophore

[1] Abe, 1934; Cayley, 1929; Howard, 1931; Wilson and Cadman, 1928.
[2] Jahn, 1911; Schunemann, 1930. [3] Schunemann, 1930.
[4] Schünemann, 1930; Von Stosch, 1935; Wilson and Cadman, 1928.
[5] Jahn, 1928*A*. [6] MacBride and Martin, 1934. [7] Gilbert, H. C., 1935.

increases in height, the ensheathing protoplasm becomes restricted to the upper portion of it. The protoplasm covering a developing sporophore may have a doubling of the number of nuclei by an equational division of each nucleus.[1] When growth of the sporophore ceases, there is a progressive cleavage (Fig. 199*A*) of the multinucleate protoplasmic sheath into uninucleate protoplasts.[2] These protoplasts lie in a single or double layer around the upper portion of the upper end of a sporophore. They lie side by side and are polygonal in outline because of mutual pressure (Fig. 199*B*). Each protoplast soon becomes broadly ellipsoidal and secretes a thin wall (Fig. 199*C*). One pole of the enclosing wall is attached to a short stalk-like projection from the sporophore. The walled uninucleate bodies borne on stalks are usually called spores. In reality they are sporangia.[1] Hence,

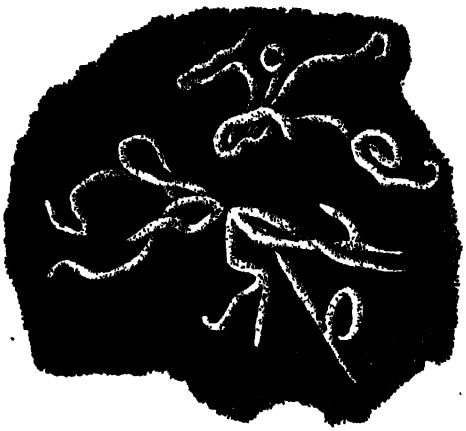


FIG. 198.—Dried fruiting body of a species of *Ceratiomyxa*. (× 20.)

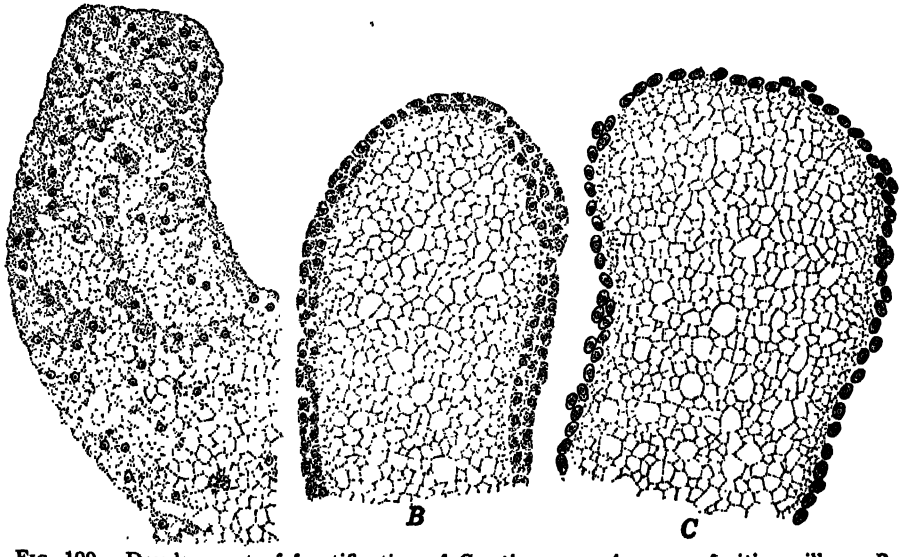


FIG. 199.—Development of fructification of *Ceratiomyxa*. *A*, young fruiting pillar. *B*, after cleavage of the protoplast. *C*, after formation of "spores." (× 325.)

one may homologize *Ceratiomyxa* with the Endosporeae by considering the fructification of *Ceratiomyxa* as an elevated hypothallus (the sporo-

[1] Gilbert, H. C., 1935. [2] Gilbert, H. C., 1935; Olive, 1907.

phore) that bears an immense number of minute stalked uninucleate sporangia.

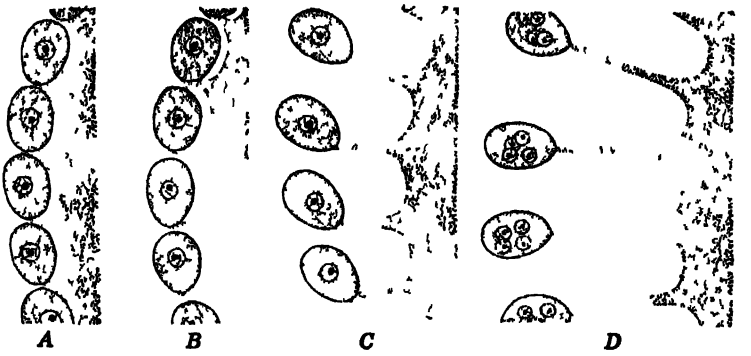


FIG 200.—Diagrams showing the progressive elevation of the spores of *Ceratiomyxa* above the sporophore (*Based upon H. C. Gilbert*, 1935.)

The stalk of a sporangium elongates to several times its original length and pushes the sporangium out from the sporophore (Fig. 200). During the course of this elongation, the orientation of the sporangium is so changed that its long axis lies parallel to the stalk.[1] Meiosis has

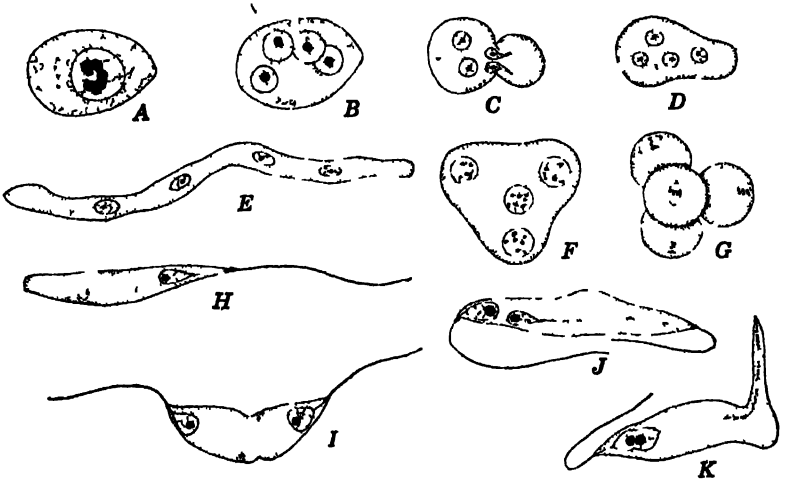


FIG. 201.—*Ceratiomyxa* sp Spore germination and gametic union *A*, uninucleate spore *B*, quadrinucleate spore *C*, spore germination *D–E*, protoplasts shortly after liberation from spore wall. *F–G*, rounding up of protoplast and cleavage into uninucleate protoplasts. *H*, gamete. *I–K*, successive stages in gametic union. (*After H. C. Gilbert*, 1935.) (*A–B*, *F–K*, × 2,250, *C–E*, × 1,500)

been described[2] as occurring in the last nuclear division before spore formation, but it is more probable that the single nucleus within a sporangium is diploid and that it divides meiotically into four daughter nuclei.[3] Meiosis is not followed by cytokinesis.

[1] Gilbert, H. C., 1935. [2] Jahn, 1936. [3] Gilbert, H C., 1935; Olive, 1907.

Succeeding stages in sporangial development are completed after detachment and dispersal of the sporangia (Fig. 201). The detached sporangium behaves like a germinating spore in that it develops a pore in the sporangial wall, and the protoplast moves out through the pore. The protoplast is globose immediately after emergence, but it soon becomes vermiform and with the four nuclei lying evenly spaced and in a linear series.[1] Within a few hours the protoplast again becomes globose. After the nuclei have become tetrahedrally arranged, there is a division into four tetrahedrally disposed uninucleate protoplasts. These naked uninucleate protoplasts are the real spores. They remain apposed to one another, and each divides into two daughter cells that are metamorphosed into uniflagellate zoogametes (Fig. 201*H*). These fuse in pairs by an approximation of their posterior poles. The spindle-shaped zygote thus formed has a single flagellum at each pole and a gamete nucleus near the point of insertion of each flagellum (Fig. 201*I*-*K*). The zygote swarms for several hours. Eventually the nucleus at one pole migrates to the opposite end of the zygote, and there fuses with the other nucleus.[1] Motility ceases soon after this and the zygote becomes globose. Its development into a plasmodium has not been followed.

CLASS 2. PHYTOMYXINAE

The Phytomyxinae have a naked, multinucleate, plasmodial type of body in which all vegetative development takes place within tissues of a host plant. Sometimes the vegetative body becomes invested with a wall at the time it divides into a mass of spores, but more often there is no formation of a wall. The plasmodium within a host cell divides directly into a mass of regularly or irregularly arranged spores. Each spore has a definite wall. A germinating spore gives rise to a single uniflagellate swarmer that may be either a zoospore or a zoogamete.

The six genera, with about 14 species, are grouped in one order (Plasmodiophorales) and family (Plasmodiophoraceae). The best-known species of the type genus (*Plasmodiophora*) is *P. Brassicae* Woronin, a parasite upon roots of various Cruciferae, especially species of the genus *Brassica*. When parasitic upon cabbages, it causes a disease popularly known both as "clubroot" and as "finger-and-toe disease." Formerly this was a disease of considerable economic importance. Today, because of discovery of methods of control, it is one of minor significance.

Infection of a cabbage root generally takes place at the seedling stage of development and by direct pentration of a uniflagellate swarm spore produced by a germinating spore (Fig. 203*E*–*F*). The swarm spores generally enter through the cell wall of a root hair,[2] but there is also

[1] Gilbert, H. C., 1935. [2] Chupp, 1917; Cook and Schwartz, 1930.

evidence that there may be a direct penetration of them into older portions of the cortex[1] of a root. A swarm spore loses its flagellum and becomes amoeboid during penetration. This amoeboid cell increases in size as it migrates about within the protoplast of the root hair, and its nucleus divides and redivides. The resultant plasmodium may have up to 30 nuclei.[2] Formation of this plasmodium takes but two or three days.[3] At any stage of growth a plasmodium developing from a swarm spore may fragment into uninucleate protoplasts, each of which becomes surrounded by a wall. These cells develop into gametangia whose nuclei divide to form four or eight daughter nuclei. This is followed by a

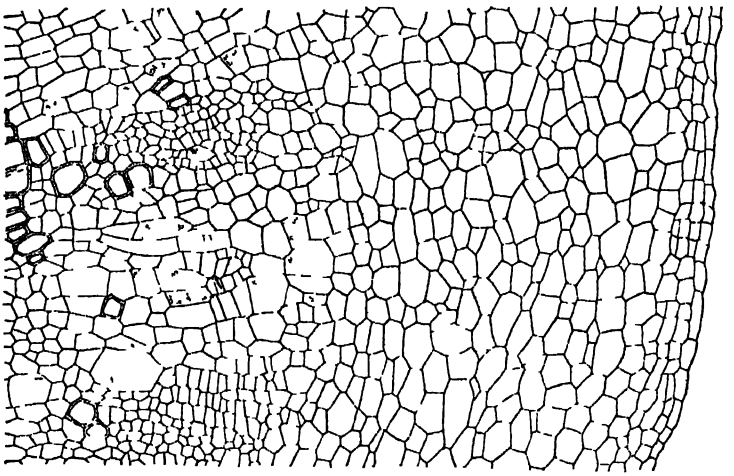


FIG. 202.—Root of a cabbage infected with *Plasmodiophora Brassicae* Woronin. (× 160.)

cleavage into uninucleate fragments, each of which is metamorphosed into a minute uniflagellate zoogamete.[4]

The zoogametes fuse in pairs to form an amoeboid zygote (myxamoeba) with a single diploid nucleus. This gametic union may take place within the root hair or after a migration of zoogametes to adjoining cortical cells.[4] The myxamoeba thus formed increases in size, and its nucleus divides and redivides a few times. These young diploid plasmodia migrate from cell to cell of the host, and some of them migrate inward to the cambium and thence up and down the root. Movement from cell to cell is by a direct perforation of cell walls.[5] After migrating vertically upward or downward through the cambium, a young plasmodium then migrates outward through the cortex. Upon reaching a cortical cell containing an abundance of food, the plasmodium remains

[1] Kunkel, 1918. [2] Chupp, 1917; Cook and Schwartz, 1930.
[3] Cook and Schwartz, 1930. [4] Cook, 1933.
[5] Chupp, 1917; Kunkel, 1918; Lutman, 1913.

within it and increases greatly in size. Up to this time the parasite has had no pronounced effect upon roots of the host. Shortly after outward migration of plasmodia from the cambial region, the cortical cells in an infected region are stimulated to divide rapidly and to enlarge to several times their normal diameter (Fig 202). This results in the greatly enlarged roots from which the disease gets its popular names Growth of the plasmodium continues until it fills the host cell (Fig 203*A–B*). Increase in size of a plasmodium is accompanied by repeated

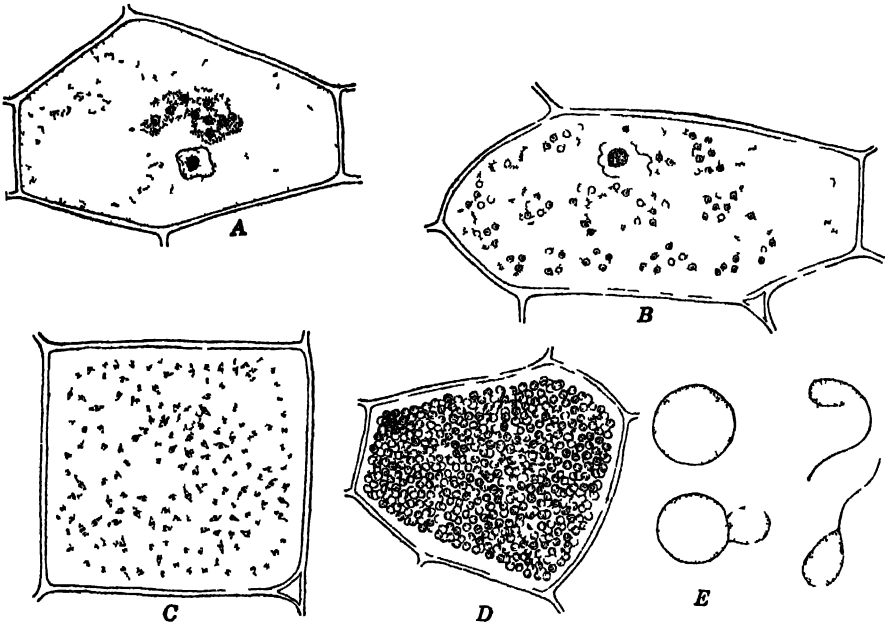


FIG. 203.—*Plasmodiophora Brassicae* Woronin *A C*, development of plasmodium within a host cell *D*, spore mass within a host cell *E*, spore germination *F*, zooid. (*E–F, after Chupp*, 1917) (*A–D*, × 650)

simultaneous division of its nuclei (Fig 203*C*) Nuclear division is equational up to the penultimate series of division The last two series of divisions are meiotic and halve the number of chromosomes in each nucleus [1] Numerous vacuoles of large and small size appear in the cytoplasm after the completion of meiosis. They become joined to one another and thus cut the plasmodium into small uninucleate fragments, each of which becomes a spherical spore with a distinct wall (Fig 203*D*).

The spores remain within the host until the latter decays. Infection of a new host takes place after germination of a spore that has remained *in situ* in the soil, and it has been shown[2] that infection does not take place unless the spore lies within a few centimeters of a seedling.

[1] Cook, 1933; Cook and Schwartz, 1930; Lutman, 1913 [2] Chupp, 1917.

CLASS 3. ACRASIEAE

The Acrasieae resemble the Myxomycetae in that they have a naked vegetative phase. They differ from the Myxomycetae in that there is never a development of a multinucleate plasmodium or of flagellate swarmers. Reproduction is preceded by an aggregation of large numbers of naked vegetative cells (myxamoebae) into a mass, the *pseudoplasmodium*, in which each myxamoeba retains its individuality. The pseudoplasmodium then changes into a fruiting body that is generally differentiated into a sterile and a fertile portion.

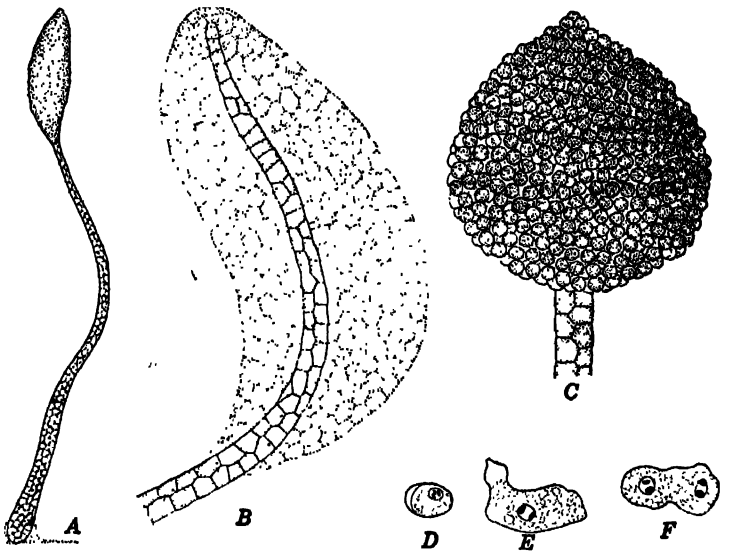


FIG. 204.—*Dictyostelium* sp. *A*, entire fructification. *B*, optical section of apex of a young sorophore. *C*, surface view of apex of an old fructification. *D*, germinating spore. *E–F*, myxamoebae. (*D–F*, *after Olive*, 1902.) (*A*, × 30; *B–C*, × 325; *D–F*, × 1,165.)

The single order of the class, the Acrasiales, contains 7 genera and about 20 species. These are divided into three families.[1]

Most of the eight or more species of *Dictyostelium* were first discovered growing upon the dung of various animals. More recently[2] it has been shown that *Dictyostelium* is also a widely distributed soil organism. The vegetative cell, the myxamoeba, is a naked amoeboid protoplast that regularly contains a single nucleus and a contractile vacuole.[3] It creeps slowly in an amoeboid manner over the substratum. Here and there on the substratum are myxamoebae that are dividing in an amoeba-like manner by constriction into two daughter myxamoebae (Fig. 204*E–F*). If environmental conditions become unfavorable, a myxamoeba may round up and secrete a wall. Such a spore-like stage

[1] Olive, 1902. [2] Raper and Thom, 1932. [3] Olive, 1902; Raper, 1935.

may germinate directly into a myxamoeba upon a return of favorable conditions. *Dictyostelium* ordinarily remains in a vegetative stage for several days after spore germination, and during this time there is a tremendous increase in the number of myxamoebae.

At the end of the vegetative period, the myxamoebae aggregate to form a pseudoplasmodium in which each of them retains its individuality. Ordinarily there is an immediate metamorphosis of the pseudoplasmodium into a fructification, but in one species[1] the pseudoplasmodium may continue movement as a single mass. In one species[2] the myxamoebae become arranged in pairs that fuse with each other just before formation of a pseudoplasmodium. This gametic union is followed by a fusion of the two nuclei. Hence in this species, and possibly in the others also, the aggregated protoplasts in a pseudoplasmodium are zygotes rather than vegetative cells.

The development of a fructification begins with a heaping up of pseudoplasmodial elements to form the base of the sterile portion (*sorophore*) of a fruiting body. Each pseudoplasmodial element (myxamoeba or zygote?) of the sorophore base becomes immobile and secretes a wall. Other elements migrate to the apex of the developing sorophore, come to rest, and also secrete a wall. The stalk thus formed above the base of a sorophore becomes narrower the higher it grows, and in the uppermost portion it is but one cell broad. The stream of pseudoplasmodial elements moving up a sorophore becomes restricted to one side of it late in the development of a stalk. Eventually, no further elements are added to the stalk apex. However, the pseudoplasmodial elements continue to stream up the stalk[3] and to accumulate in a globose mass at its apex (Fig. 204*A–B*). After migrating to the stalk apex each element rounds up, secretes a wall, and becomes a spore. Collectively they constitute the fertile portion (*sorus*) of a fruiting body (Fig. 204*C*).

The spores are readily detachable from a sorus, and they may germinate immediately after dispersal if conditions are favorable. Upon germination there is a rupture of the spore wall and an amoeboid escape of the protoplast from the wall. The protoplasts thus liberated are the first myxamoebae of the next vegetative generation.

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[1] Raper, 1935. [2] Skupienski, 1918.
[3] Harper, 1926; Olive, 1902; Raper, 1935.

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CHAPTER X

EUMYCETAE—INTRODUCTION

The Eumycetae, the true fungi, are saprophytic or parasitic plants that are without photosynthetic pigments. They differ from most colorless algae in that they accumulate carbohydrate reserves as glycogen instead of as starch. The Eumycetae differ from the Myxothallophyta in that there is almost always a definite cell wall throughout all stages of vegetative development. The cell wall is generally a carbohydrate and variously composed of cellulose, callose, pectose, or related compounds. Many of the lower Eumycetae (the Phycomycetae) have a wall in which cellulose predominates. Advanced members of the division (Ascomycetae and Basidiomycetae) have a cell wall predominantly composed of the carbohydrate known as *fungus cellulose* or *chitin*. All but the most primitive of the Eumycetae have the branching filamentous type of plant body known as a *mycelium* in which a single filament or branch is termed a *hypha*. The mycelium may consist of a single multinucleate cell (a *coenocyte*) in which there are no transverse walls; or it may have numerous cross walls dividing it into uni-, bi-, or multinucleate cells. The various hyphae of a mycelium may lie in an amorphous felt-like mass, or they may be intertwined to form a macroscopic mass of definite form. In the latter case the mycelium is generally multicellular and with all or some of the hyphae compacted into a pseudoparenchymatous tissue.

The Eumycetae, exclusive of the lichens, include some 75,000 species distributed among 2,850 genera. Some species are strictly parasitic, some strictly saphrophytic, some are parasitic at one stage of development and saprophytic at another, and still other species may grow either saprophytically or parasitically. The living organism upon which a parasite grows may be a plant or an animal. Plants parasitized by Eumycetae range from the simplest algae to the most advanced angiosperms. In some cases a particular species is restricted to a single host species; in others it may be parasitic upon several distantly related hosts. A few saprophytic species are aquatic in habit, but the great majority of them are terrestrial and grow either in soil or upon remains of plants or animals.

If conditions are favorable, most Eumycetae have the plant body (thallus) forming reproductive bodies after it has attained a certain stage

of development. Some primitive members of the group have a transformation of the entire thallus into reproductive bodies. Generally, however, only a portion of the plant body is thus transformed, and the remainder continues in the vegetative state. Reproductive bodies may be sexual or asexual in nature.

Asexual Reproduction. Asexual reproductive bodies are called *spores*. Certain types of them (ascospores and basidiospores) are formed at a specific time in the life cycle and immediately following a reduction division Other types of spores are purely vegetative in nature and give rise to a mycelium identical with that producing them. Some types of vegetative spores are formed directly on a hypha; others are formed within special spore-producing organs known as *sporangia*. Discussion of the various types of spores will be postponed until succeeding chapters.

Sexual Reproduction. Taken as a whole, the sexual reproductive bodies of the Eumycetae show the same evolutionary changes as have already been noted in the Chlorophyceae and Phaeophyta. In the most primitive Phycomycetae there is a union of two flagellated gametes (*zoogametes*) of equal size. A condition somewhat in advance of this *isogamy* is the union of two zoogametes of unequal size (*anisogamy*). The smaller gamete of an anisogamous pair is male, and the larger is female. Anisogamy leads in turn to *oogamy*. Here the female gamete (the *egg*) is always large and immobile The male gamete is always much smaller than the egg and either a flagellated motile *antherozoid* or a nonflagellated *aplanogamete* The isogamous sexual reproduction by a union of two nonflagellated gametes (aplanogametes) characteristic of certain Phycomycetae probably represents a retrogression from oogamy.

The gametes of most Eumycetae are formed within special cells, the sex organs. Strictly speaking, all such cells should be called gametangia, but the term gametangium is generally restricted to the sex organs of isogamous and anisogamous species. The male gametangium of an oögamous species is called an *antheridium* and the female gametangium an *oogonium*.

In the most primitive class of Eumycetae, the Phycomycetae, the product of gametic union is a *zygote*. It generally becomes surrounded by a thick wall and enters upon a period of rest. Zygotes of many, if not all, phycomycetes have a union of the nuclei contributed by the two gametes. It is very probable, although not so definitely established, that the fusion nuclei of Phycomycetae undergo a reduction division before a zygote germinates.[1]

The zygote, or the morphological equivalent of it, of the Ascomycetae and the Basidiomycetae does not secrete a wall and enter upon a period

[1] This is not the case in one exceptional genus (*Allomyces*, page 384).

of rest; neither is there a reduction division before it begins development into a succession of cell generations that are diploid. Production of diploid cells terminates with the formation of a special cell (ascus or basidium) in which there is a reduction division of a diploid nucleus. A more complete discussion of the rather complicated developmental changes following gametic union in Ascomycetae and Basidiomycetae will be given in Chaps. XII and XIII.

Origin of the Eumycetae. There are two conflicting theories concerning the origin of the true fungi. According to one theory, they are derived from algae; according to the other theory, they are derived from protozoa. Adherents of the algal theory hold that the Phycomycetae are Chlorophyceae which have lost their chlorophyll and thus changed from an autotrophic to a heterotrophic mode of nutrition. They hold that change in method of nutrition has not been accompanied by changes in method of sexual reproduction and point to the marked similarity of this in oögamous Chlorophyceae and Phycomycetae. Such a derivation of the Phycomycetae overlooks the fact that there are fundamental differences between Phycomycetae and the known Chlorophyceae which regularly lack chlorophyll. Saprophytic or parasitic Chlorophyceae regularly have an accumulation of reserve carbohydrates as starch, just as do the Chlorophyceae with chlorophyll. On the other hand, Phycomycetae never accumulate starch and generally accumulate carbohydrates as glycogen. Zoospores and zoogametes of green algae are never uniflagellate. Those of a majority of the chytrids (the most primitive of all Phycomycetae) and those of certain mycelial Phycomycetae regularly have zoospores or zoogametes with a single flagellum. If, as seems to be the case, the metabolism and the type of flagellation are characters of fundamental importance, the ancestry of the phycomycetes is to be sought among the uniflagellate protozoa rather than among the green algae.

Even if one derives the Phycomycetae from the Protozoa, there still remains the question of the origin of the Ascomycetae. There are striking similarities in the structure of sex organs and the structures developed subsequent to gametic union in the Ascomycetae and the Rhodophyceae (page 422). Because of this, many think the ascomycetes immediately derived from the red algae. However, there are equally good reasons for thinking that the distinctive reproductive features common to the two groups have been evolved along independent phyletic lines.

Evolution among the Eumycetae. The Eumycetae are a series of considerable antiquity, for indubitable phycomycetes have been found in the Devonian and parasitic upon the oldest known pteridophytes, the Psilophytales.

The chytrids stand at the bottom of the phycomycetan series. They are mostly aquatic in habit, often with the whole plant body fertile, and reproducing sexually by free-swimming zoogametes of equal size. Two series with a mycelial type of plant body appear to have been evolved from the chytrids; one reproducing by means of uniflagellate swarmers, the other by biflagellate ones (Fig. 205). In both series there is a progressive evolution to oögamy. The uniflagellate series is strictly aquatic.

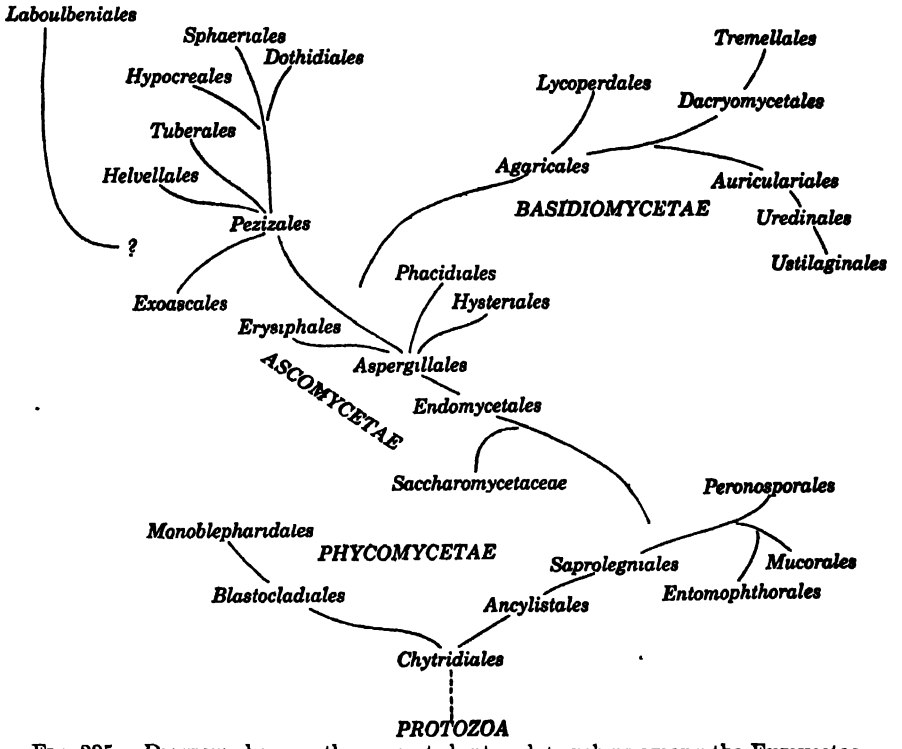


FIG. 205.— Diagram showing the suggested interrelationships among the Eumycetae.

Primitive members of the biflagellate series are aquatic; advanced members are terrestrial. Phycomycetes parasitic upon land plants are generally oögamous and are always without motile gametes. They may or may not produce flagellated asexual spores. In the zygomycetes, a retrogressive series from the oögamous land forms, there are no flagellated reproductive bodies.

The Ascomycetae appear to have arisen among the oögamous Phycomycetae. The most primitive ascomycetes have a solitary naked ascus developed directly from a zygote (page 424). More highly developed ascomycetes have a number of asci developed indirectly from a zygote. When a number of asci are formed, they are always surrounded by a common envelope of sterile tissue. The simpler genera with a number

of asci have them irregularly arranged within the envelope; in more advanced genera the asci are regularly arranged.

The basidium, the characteristic feature of the Basidiomycetae, probably arose by modification of an ascus (page 472). It is probable, also, that this modification took place among somewhat advanced rather than among primitive ascomycetes. The simplest of the basidiomycetes appear to be those in which the basidium is undivided. Evolution from this type seems to have been in two series: one characterized by a vertically divided basidium, the other by a transversely divided basidium.

Classification. Mycologists are in universal accord in dividing the true fungi into four classes. Some also include the Myxomycetae among the fungi but, for reasons already mentioned (page 351), the myxomycetes seem to be a series coordinate in rank with the Eumycetae. The four classes of Eumycetae are:

Phycomycetae in which the mycelium is generally unseptate but may be transversely septate. The spores are produced in indefinite numbers within a sporangium. In most members of the class the gametic union results in a zygote that forms a thick wall and enters upon a period of rest.

Ascomycetae in which the characteristic reproductive organ, the ascus, produces spores in a unique manner and immediately after a reduction division. The number of spores in an ascus is a multiple of two and is generally eight.

Basidiomycetae in which the distinctive reproductive organ, the basidium, produces a definite number of spores (frequently four), each of which is borne externally on a short stalk

Fungi imperfecti in which a production of neither ascospores, basidiospores, nor zygotes has as yet been discovered in the life cycle. This class is a provisional repository for species that cannot be referred with certainty to one of the three foregoing classes.

CHAPTER XI

PHYCOMYCETAE

The Phycomycetae, unlike Basidiomycetae and Ascomycetae, do not produce one distinctive type of spore. Phycomycetes reproduce asexually by means of sporangiospores that are formed in indefinite numbers within a sporangium. In many, but not all, members of the class there is a union of gametes to form a zygote that secretes a thick wall and enters upon a rest period. Most of the genera have unseptate multinucleate mycelia, but some have a mycelium that is regularly transversely septate. There are also genera in which the vegetative portion of the plant body is not a true mycelium. The class includes approximately 130 genera and 1,500 species.

Many genera are aquatic parasites or saprophytes. Others are nonaquatic and either parasitic or saprophytic. Mycelial development may be extensive in both saprophytic and parasitic genera, but in neither of them is there a production of a thallus of definite macroscopic form.

Asexual Reproduction. Most members of the class reproduce asexually by means of sporangiospores that are formed within sporangia. Sporangiospores are formed by a cleavage of the contents of a sporangium into an indefinite, and sometimes large, number of protoplasts. This method of spore formation is quite unlike that in sporangia (asci) of ascomycetes, where a definite number of spores is delimited within the protoplast. The protoplasts formed by cleavage within sporangia of Phycomycetae may develop one or two flagella and thus become *zoospores*, or they may secrete walls and become *aplanospores*. A given species generally produces only zoospores or only aplanospores. In a few exceptional species, and depending upon environmental conditions, either zoospores or aplanospores may be formed. Phycomycetes that regularly form zoospores are generally more primitive than those that regularly form aplanospores.

Certain of the more advanced families form spore-like structures that become detached from the hyphae producing them. These are usually called *conidia* and the hyphae bearing them *conidiophores*. This terminology is open to question since they are not homologous with the conidia and conidiophores of ascomycetes and basidiomycetes. Instead, they seem to be small detachable sporangia that are dispersed by wind. For this reason the name *conidiosporangium* is more appropriate. Ger-

minating conidiosporangia of certain species form one or several zoospores. Those of other species function in a manner similar to aplanospores and germinate directly. Among the Mucorales there are certain genera in which the spores lie in a linear series within the sporangium and in which the sporangial wall eventually disintegrates. Sporangiospores of these fungi bear a superficial resemblance to conidiophores that have cut off a succession of conidia.

Mycelia that have become transversely septate may have certain cells becoming thick-walled. These spore-like cells, which are generally intercalary, are comparable to the akinetes of green algae. The akinetes of phycomycetes and other fungi are known as *chlamydospores*.

Sexual Reproduction. Most of the Phycomycetae are known to reproduce sexually, and it is not improbable that this will also be discovered among the genera where it has not been noted as yet. Homothallism appears to be of more widespread occurrence among the Phycomycetae than is heterothallism. The discovery[1] that fungi may be homothallic or heterothallic was made during studies upon certain Mucorales.

In a few genera the gametes are produced within undifferentiated cells. Generally, however, they are formed in highly differentiated gametangia. Gametic union may be *isogamous* and either by a fusion of two morphologically similar uni- or biflagellate gametes (*zoogametes*) or by a fusion of two similar nonflagellated gametes (*aplanogametes*). Gametic union may also be *heterogamous* with a fusion of two gametes dissimilar in size. In very rare cases, as *Allomyces javanicus* Kniep, the heterogamy is *anisogamous* with both gametes flagellated. More often it is *oögamous* with a union of a small flagellated male gamete (the *antherozoid*), or a small nonflagellated male gamete, with a large immobile female gamete—the *egg*. The male gamete is produced within an *antheridium* and the egg within an *oogonium*. In some phycomycetes both gametes are uninucleate; in others one is uninucleate and the other multinucleate; in still others both gametes are multinucleate. Many species with both gametes uninucleate have been shown to have a fusion of the two nuclei in the young zygote. It is also definitely established that, when a uninucleate male gamete unites with a multinucleate egg, its nucleus fuses with one of those in the egg. There is considerable uncertainty as to what happens when both gametes are multinucleate, but it is thought that male and female nuclei unite in pairs.

The zygote formed by union of two gametes generally secretes a thick wall and enters upon a period of rest. Upon germination it may form one to several zoospores, or zoospore formation may be omitted and there may be a direct development of a hyphal outgrowth by the germinating zygote. This hypha may develop into an extensive myce-

[1] Blakeslee, 1904.

lium, or it may grow to a very limited extent and then produce one or more sporangia.

Life Cycle of Phycomycetes. It is very probable that most Phycomycetae have a reductional division of the fusion nucleus before or at the time of zygote germination. This has been definitely established for certain species in which there is a fusion of two uninucleate gametes. If these species have a multinucleate mycelium and a uninucleate zygote, the life cycle is comparable to that of green algae in which a many-celled haploid generation alternates with a one-celled diploid phase. In at least one phycomycete (*Allomyces*) there is an alternation of a spore-producing generation with a gamete-producing generation. Nuclei in the alternating sexual and asexual generations of this fungus are thought[1] to be respectively haploid and diploid, but this assumption is based upon the relative size of the nuclei rather than counts of their chromosomes.

Origin and Evolution of Phycomycetes. There are many who hold that the Phycomycetae are derived from the Chlorophyceae. In fact, literal translation of the name coined when the class was established by DeBary[2] means algal fungi. The chief reason for deriving the phycomycetes from the green algae is the great similarity in sexual reproduction of the oogamous Phycomycetae (the oomycetes) and the oogamous Chlorophyceae. Suggested algal ancestors of the oomycetes include *Cylindrocapsa*[3] and *Vaucheria*.[4] Some of those advocating a chlorophycean origin hold that this has been polyphyletic and that the isogamous aplanogametic Phycomycetae (the zygomycetes) and the chytrids originated independently from the oomycetes. The Zygnematales have been suggested as a possible starting point for the zygomycetes[5] and the Chlorococcales as the starting point for the chytrids.[6] A polyphyletic origin from algae is also implied in the old systems of classification[7] that grouped algae and fungi together in classes differing from one another in method of reproduction. Some modern adherents[8] of this idea go so far as to refer the phycomycetes to orders named from the algae (for example, Protococcales, Spirogyrales, Vaucheriales, Confervales).

Others[9] think that the Phycomycetae are derived from the Protozoa. Those believing in this theory hold that the chytrids are the most primitive of the phycomycetes and are not retrogressive from the oomycetes. Arguments cited in support of this include sexual reproduction by motile isogametes and the simple structure of the plant body. It is also held that the flagellated zoospores and gametes of chytrids bear a much

[1] Kniep, 1930. [2] DeBary in Fuckel 1869–1875 [3] DeBary, 1881.
[4] Von Tavel, 1892. [5] Von Tavel, 1892; Vuillemin, 1912
[6] Davis, 1903; Griggs, 1912; Kusano, 1912; Lagerheim, 1893
[7] Cohn, 1872; Sachs, 1874. [8] Clements and Shear, 1931.
[9] Fischer, 1892; Dangeard, 1886, 1903; Atkinson, 1909; Cavers, 1915; Cook, 1929.

closer resemblance to protozoa than they do to zoospores and motile gametes of green algae. The chief argument for this is the uniflagellated swarmer found in most chytrids. Such motile cells are common among the protozoa and unknown among the green algae. Taken by itself the type of flagellation would not be a justification for a derivation from the protozoa, but this correlates with other characters, including metabolism of the protoplast.

As between the two theories, that of a derivation from the Protozoa seems the more probable. The most primitive series among the phycomycetes (the chytrids) is usually considered a monophyletic one, but there is a possibility that it is polyphyletic in origin. In any case, there appear to be two phyletic lines leading from the chytrids. Both have mycelial plant bodies, but one reproduces by uniflagellate swarmers, the other by biflagellate ones. Sexual reproduction in the uniflagellate series of mycelial phycomycetes shows an advance from the anisogamy found in the Blastocladiales to a true oogamy found in the Monoblepharidales. The simplest members among the biflagellate mycelial phycomycetes (the Ancylistales) are oogamous and have a fusion of two aplanogametes of different size. Evolutionary changes in sexual reproduction of more advanced members of this series (Saprolegniales, Peronosporales) are along the line of a higher differentiation of the two aplanogametes. The zygomycetes cannot be referred to either series with certainty because they never form motile reproductive cells. However, their affinities seem to lie with the biflagellate series. It is not improbable that their aplanogamic isogamy represents a retrogression from the aplanogamic oogamy found in oomycetes with biflagellate zoospores.

Classification. The filamentous Phycomycetae are generally divided in two orders, the Oömycetae and the Zygomycetae. The chytrids may or may not be included as a third order. The placing of all oogamous phycomycetes in one order is decidedly artificial, and it obscures the probability that oogamy has arisen in independent phyletic lines among the phycomycetes. The same is true, but to a more limited extent, when all zygomycetes are placed in a single order. The recent[1] reclassification of the Phycomycetae into a number of orders, instead of into Oomycetae and Zygomycetae, seems to be a much more natural arrangement. When the chytrids are included among the Phycomycetae, the class may be divided into eight orders.

ORDER 1. CHYTRIDIALES

The Chytridiales have a unicellular plant body that is never a true mycelium. In most cases all or the major portion of the plant body develops into a single sporangium or gametangium, but there may be a

[1] Fitzpatrick, 1930.

formation of several reproductive organs. Asexual reproduction is by means of uni- or biflagellate zoospores. Sexual reproduction is by a fusion of flagellate isogametes. The order includes some 45 genera and 275 species.

A few members of the order are saprophytes, the others are parasites. Many of the parasitic genera grow upon aquatic phycomycetes or upon fresh-water algae. There are also some Chytridiales that are parasitic upon terrestrial angiosperms. A very few species are parasitic upon marine plants.

In most cases the parasite is restricted to one cell of the host. If the body of a chytrid is not differentiated into fertile and vegetative portions (as in Olpidiaceae, Woroninaceae, and Synchytriaceae), it lies wholly within one host cell. Other Chytridiales (the Rhizidiaceae) have the plant body differentiated into a single globose fertile portion and a rhizoidal vegetative portion in which the branches gradually taper to a hair-like tip. The fertile portion of such a thallus may lie external to the host cell or within it. In still other chytrids (the Cladochytriaceae) the plant body is a gradually attenuated system of rhizoidal branches in which fertile areas are developed at various points in the branching system. Such a thallus has been called[1] a *rhizomycelium.* Some chytrids, as *Synchytrium,* have a protoplast that remains uninucleate until shortly before reproduction; others, as *Olpidium,* have the number of nuclei increasing as the protoplast grows in size. All chytrids are multinucleate at the time of reproduction and with either a progressive or simultaneous cleavage of the protoplast into uninucleate zoospores or gametes.

The structure of the plant body, the structure of the flagellated reproductive cells, and the mode of germination are the bases upon which the order is divided into families. The phyletic relationships between the various families are obscure, and it is impossible to hazard a guess as to which is the most primitive. There is equal uncertainty as to whether or not the order is a monophyletic series. However, there is a general agreement that the Synchytriaceae and the Cladochytriaceae are more highly specialized than are other families. The order is divided into five families.

FAMILY 1. RHIZIDIACEAE

The Rhizidiaceae have a plant body differentiated into a single globose fertile portion and a vegetative portion of gradually attenuated rhizoidal branches. Most members of the family have the fertile portion external to the host cell, but some of them have it within the host. Reproduction is by division of the fertile portion into uniflagellate

[1] Karling, 1931, 1932.

zoospores or gametes. The family contains about 20 genera and 100 species.

Rhizophidium is an aquatic genus with about 30 species. Unlike most other Chytridiales, the genus is found in both fresh and salt water. Two marine and twelve fresh-water species have been recorded from the United States. Most of the fresh-water species are parasitic and grow upon algae, upon other aquatic fungi, or upon pollen grains. One species is saprophytic and grows on submerged decaying twigs.

The fertile portion of the plant body is more or less globose, surrounded by a distinct wall, and lies external to the host cell. The

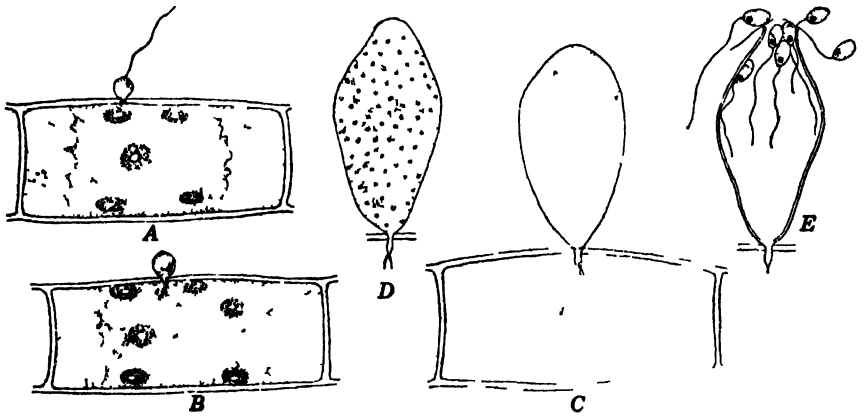


FIG 206.—*Rhizophidium ovatum* Couch *A–B*, early stages in germination *C*, mature plant body *D*, cleavage into zoospores *E* liberation of zoospores (*After Couch*, 1935.) (× 1,250)

vegetative portion is naked and consists of delicate, attenuated, rhizoidal branches that ramify through the protoplast of the host (Fig 206*A–C*)

At the time of reproduction[1] the contents of the reproductive portion cleave into many angular protoplasts, each of which is metamorphosed into a uniflagellate swarmer (Fig 206*D-E*). These escape through one or more pores in the wall. All swarmers may swim out within a few seconds after the pore opens,[2] or they may creep out slowly in an amoeboid manner and then swim away. The uniflagellate swarmers may be zoospores or zoogametes. Zoospores swim about with their flagella trailing behind. When one of them comes to rest upon a host cell, it may do so with the flagellated end upward. In such a case the flagellum disappears and a delicate rhizoidal outgrowth grows into the host from the other end of the fungus (Fig. 206*A*). The fertile portion of the fungus that lies external to the host secretes a wall and increases rapidly in size Development to maturity of *R. ovatum* Couch may be completed within 20 hours.[2]

[1] Couch, 1932 [2] Couch, 1935.

Sexual reproduction of *R. ovatum* is by means of uniflagellate gametes of equal size. A male gamete comes to rest upon the host, loses its flagellum, and sends a delicate rhizoid into the host in the same manner as a germinating zoospore [1] Shortly afterward a female gamete becomes applied to the male gamete and loses its flagellum (Fig. 207). Both of the apposed gametes increase greatly in size and secrete a wall. As enlargement continues, the contents of the male cell migrate into the female cell, and the two nuclei unite The spherical zygote borne upon

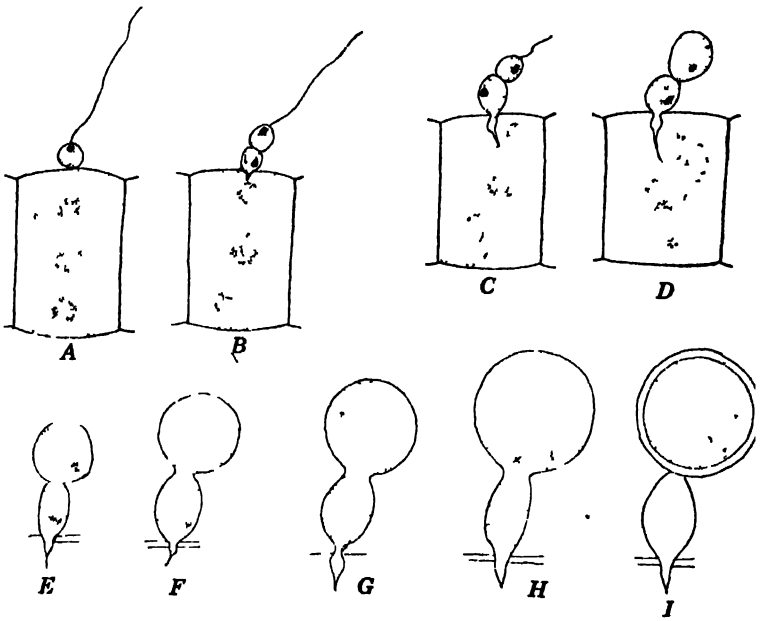


FIG 207 – *Rhizophidium ovatum* Couch *A*, male gamete *B–D*, gametic union. *E H*, stages in gradual enlargement of zygotes *I*, mature zygote (*After Couch*, 1935) (× 1,875)

the empty male cell secretes a fairly thick wall This zygote may germinate to form zoospores within two or three days.[1]

FAMILY 2. OLPIDIACEAE

In the Olpidiaceae the entire plant body of the fungus lies within the host cell, and all of it is fertile. It reproduces by means of uniflagellate swarmers that may be either zoospores or zoogametes The naked swarmer comes to rest upon the host and secretes a thin wall. The protoplast of this cell then migrates into the host and there continues development. The family includes about eight genera and 50 species.

Olpidium, the largest genus of the family, has about 25 species. These grow on a variety of hosts, including fresh-water algae, other

[1] Couch, 1935.

aquatic fungi, pollen grains, and the epidermal cells of vascular land plants. The most thoroughly investigated species is *O. Viciae* Kusano, a parasite infecting epidermal cells of leaves and stems of *Vicia unijuga* A. Br. Development of the fungus may be rapid and into a thin-walled cell (the "summer spore") or slow and into a thick-walled cell (the "winter spore").[1] The uniflagellate swarmers produced by the summer spore are generally called zoospores, but it is more probable that they are gametes which may develop parthenogenetically into other haploid summer spores or unite in pairs and develop into diploid winter spores.

A young summer spore within a host cell is a naked globose mass of protoplasm. If there has been but a single infection of a host cell, the

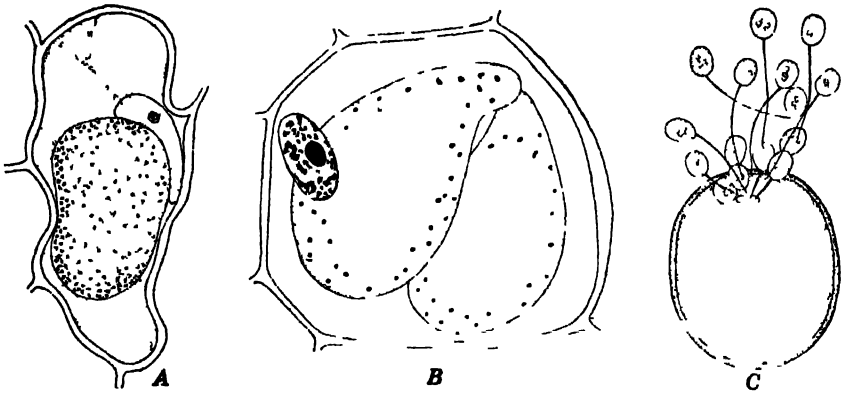


FIG. 208.—*Olpidium Viciae* Kusano. *A–B*, stages in development of summer spores. *C*, liberation of zooids from a summer spore (*After Kusano*, 1912) (*A*, × 500, *B*, × 900; *C*, × 800.)

fungus may increase in size until it fills almost all of the cell (Fig. 208*A–B*). Increase in size of the fungus is accompanied by a repeated division of its nuclei.[1] The wall surrounding the parasite is not plainly evident until late in its development. After a few days, and when the fungus is nearly mature, there is a development of a small beak-like outgrowth, the future *exit tube*, that grows through the host cell wall. Soon after this the whole protoplast of the fungus becomes divided into a large number of uniflagellate swarmers. The tip of the beak-like exit tube ruptures suddenly, and the swarmers swim out with their flagella trailing (Fig. 208*C*). Under favorable conditions the cell becomes empty within two or three minutes. At the end of the free-swimming period, the swarm spore creeps over the surface of the host in an amoeboid fashion, comes to rest, assumes a spherical form, and secretes a thin wall. The protoplast of this small cell soon sends forth a naked haustorial outgrowth that grows through the underlying host cell wall; this is followed by a migration of the entire protoplast into the host cell.

[1] Kusano, 1912.

Sexual reproduction of *O. Viciae* is by means of uniflagellate zoogametes produced by the summer spores.[1] Certain other species of *Olpidium* are also known[2] to have a similar fusion of gametes. Union of gametes takes place while both are motile, and the resultant biflagellate zygote remains motile for some time (Fig 209*A*). It eventually comes to rest upon the host and becomes invested with a thin wall. Its protoplast also sends out a haustorium that perforates the host cell wall, and this is followed by a migration of the protoplast of the zygote into the host cell

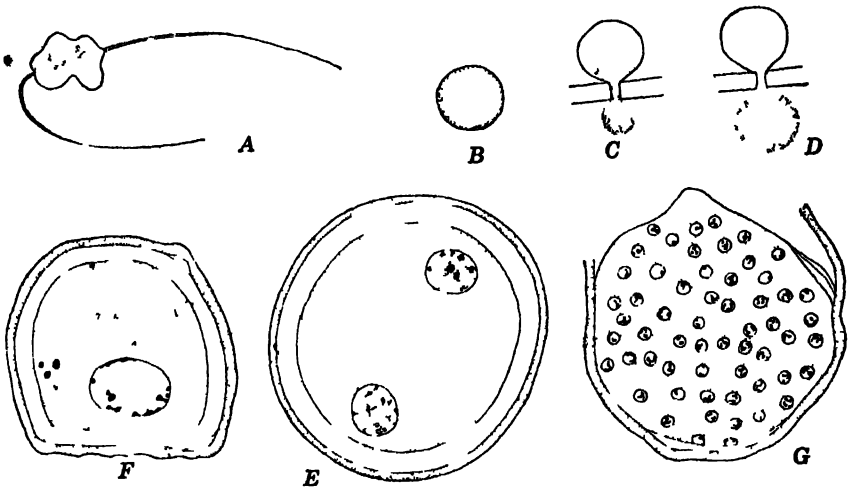


FIG 209.—*Olpidium Viciae* Kusano, gametic union and development of the winter spore *A*, gametic union *B D*, germination of zygotes *E F*, overwintering stages before and after union of the nuclei *G*, multinucleate stage just before germination (*After Kusano* 1912) (*A D*, × 1,200, *E G*, × 1,350)

(Fig 209*B D*). This protoplast contains the two nuclei derived from the two gametes. The resemblance between infection by zoospores (or parthenogenetic gametes) and zygotes ceases at this stage A protoplast originating through gametic union enlarges considerably, secretes a thick wall, and enters upon a rest period that lasts until the next spring. The two gamete nuclei enlarge considerably but do not fuse with each other until the next spring (Fig 209*E F*). When they do unite, there is an almost immediate division and redivision of the zygote nucleus (Fig. 209*G*). It is very probable that the first divisions are reductional. The contents of the thick-walled, multinucleate, winter spore then cleave to form a number of uniflagellate zoospores These swarm and then germinate to form summer spores

FAMILY 3. SYNCHYTRIACEAE

The Synchytriaceae have the entire plant body lying within a host cell, surrounded by a wall, and all of it developing into either a thin- or a

[1] Kusano, 1912 [2] Cook and Collins, 1935

thick-walled, spore-like cell that eventually forms a number of aplanospores. Upon germination each aplanospore produces a number of uniflagellate zoospores or zoogametes. There are two or three genera in the family and about 75 species.

Synchytrium, a genus with about 70 species, is a widely distributed parasite in epidermal cells of various angiosperms. Most species cause

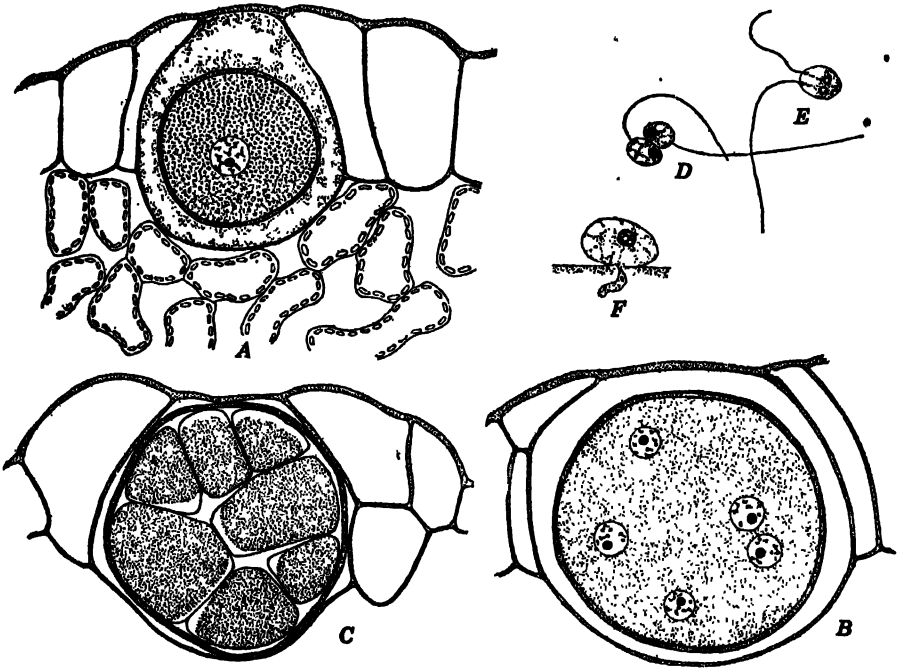


FIG. 210.—*A–C*, Summer spores of *Synchytrium* sp. *A*, uninucleate stage. *B*, multinucleate stage. *C*, after cleavage into aplanospores. *D–F*, *S. endobioticum* (Schilb.) Perc. *D–E*, gametic union. *F*, germination of zygote. (*D–F*, *after Curtis*, 1921.) (*A-C*, × 325; *D–F*, × 2,000.)

a gall-like swelling of the infected host tissue (Fig. 210*A*). In some species the mature fungus is always surrounded by a thick wall; in others it may be surrounded by either a thin or a thick wall. For certain of these latter species, it is definitely established that the thick-walled fungus cell (the winter spore) develops from a zygote and that production of the thin-walled fungus cell (the summer spore) is not preceded by gametic union.[1]

A cell developing into a summer spore is uninucleate until it has grown to nearly full size. Enlargement of the fungus is accompanied by a conspicuous increase in size of the nucleus (Fig. 210*A*). As the fungus approaches maturity, its nucleus enters upon a series of divisions (Fig. 210*B*). This may be followed by a progressive cleavage that cuts it

[1] Curtis, 1921; Kusano, 1930; Köhler, 1931.

up into many uninucleate protoplasts,[1] or into several multinucleate protoplasts.[2] The protoplasts thus formed become rounded and secrete a wall (Fig. 210*C*). These bodies are usually called *sporangia*, and the mass of them a *sorus*. However, from the morphological standpoint, they are aplanospores. Whether uninucleate or with several nuclei when first formed, each aplanospore eventually contains a large number of nuclei. When an aplanospore germinates, its protoplast divides to form a large number of uniflagellate zoogametes. In most cases the gametes develop parthenogenetically into thin-walled summer spores. At the time of infection, the zoogamete migrates directly through the host cell in an amoeboid fashion.

Conjugation (Fig. 210*D–E*) of gametes takes place outside the host and either while both gametes are motile[2] or after one of the conjugating pair has lost its flagellum.[3] Conjugation is followed by an immediate fusion of the two gamete nuclei and an amoeboid migration of the naked zygote into the host cell (Fig. 210*F*). There it develops into a thick-walled uninucleate winter cell. When a winter spore germinates in the following spring, its protoplast becomes multinucleate. This may be followed by a division into a large number of uniflagellate zoospores or into several multinucleate aplanospores each of which forms many zoospores upon germination.

FAMILY 4. CLADOCHYTRIACEAE

The Cladochytriaceae have a rhizomycelial type of plant body that may ramify through several host cells. Here and there the vegetative portion of the plant body is enlarged into spindle- or top-shaped *spindle organs*. A rhizomycelium also bears several terminal or intercalary sporangia that produce uniflagellate zoospores. Sexual reproduction is of extremely rare occurrence and takes place by a fusion of uniflagellate zoogametes.

The type genus *Cladochytrium* grows parasitically upon Chlorophyceae, Charophyceae, and certain aquatic angiosperms. There are a half dozen or more species, and certain of these have been cultivated[4] under saprophytic conditions. The rhizomycelium consists of gradually attenuated branches that usually extend through several adjoining host cells (Fig. 211*A*). Here and there in the rhizomycelium are more or less spindle-shaped enlarged portions, the spindle organs or *turbinate organs*. They are purely vegetative in nature, but their precise function is uncertain. One suggested function is that of a center for reduplication of the rhizomycelium.[5] The spindle organ is usually blocked off from the remainder of the thallus by transverse septa, and it may be divided into two or more cells by transverse walls.

[1] Harper, 1899. [2] Curtis, 1921 [3] Kusano, 1930.
[4] Karling, 1935. [5] Karling, 1931.

A mature rhizomycelium generally has several sporangia. These may develop either at the tips of the branches or some distance back from a branch tip. Sporangial development (Fig. 211*A*) begins with a localized swelling of the rhizomycelium.[1] Enlarging sporangia are club-shaped, but fully developed ones are globose and with one or more tubular outgrowths, the future exit tubes. The mature sporangium is invested with a distinct wall that delimits it from the remainder of the rhizomycelium. The protoplast within a sporangium cleaves progressively[2] to form a number of uniflagellate zoospores that are discharged through

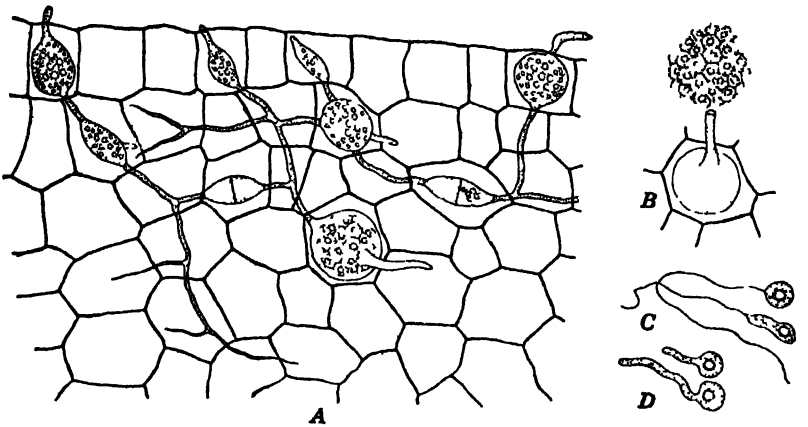


FIG. 211.—*Cladochytrium replicatum* Karling. *A*, thallus in leaf of *Eriocaulon septangulare* With. *B*, spore discharge from a sporangium. *C*, zoospores. *D*, germinating zoospores. (*After Karling*, 1931.)

the exit tube (Fig. 211*B*). Sometimes[3] the sporangium develops a very thick wall and functions as a resting spore. Upon germination these resting sporangia produce zoospores that are discharged through a newly formed exit tube.[4] Infection of the host seems to be by a zoospore coming to rest, losing its flagellum, and forming a germ tube that grows directly into a host cell (Fig. 211*C–D*).

Sexual reproduction has never been observed in *Cladochytrium*. Fusing pairs of uniflagellate swarm spores have been observed in another genus of the family.[5]

FAMILY 5. WORONINACEAE

Genera assigned to the Woroninaceae have a plant body that is parasitic upon a single host cell and one in which the whole thallus is fertile. Different from all other Chytridiales, reproduction of the Woroninaceae is by biflagellate zoospores. One genus (*Olpidiopsis*) is known to reproduce sexually by means of aplanogametes of unequal size. The family includes about 4 genera and 15 species.

[1] Karling, 1931. [2] Karling, 1937. [3] Karling, 1935; Sparrow, 1931.
[4] Karling, 1935. [5] Karling, 1934.

Olpidiopsis is a genus with about five species, all of them parasitic upon Saprolegniales. The thallus of *Olpidiopsis* is an ellipsoidal protoplasmic mass that lies wholly within the host. Growth of the plant body is accompanied by a continued increase in the number of nuclei,[1] and it does not become invested with a wall until it is almost mature (Fig. 212*A–B, D*).

Asexual reproduction is by a cleavage of the cell contents into uninucleate protoplasts (Fig. 212*C*), each of which is metamorphosed into a

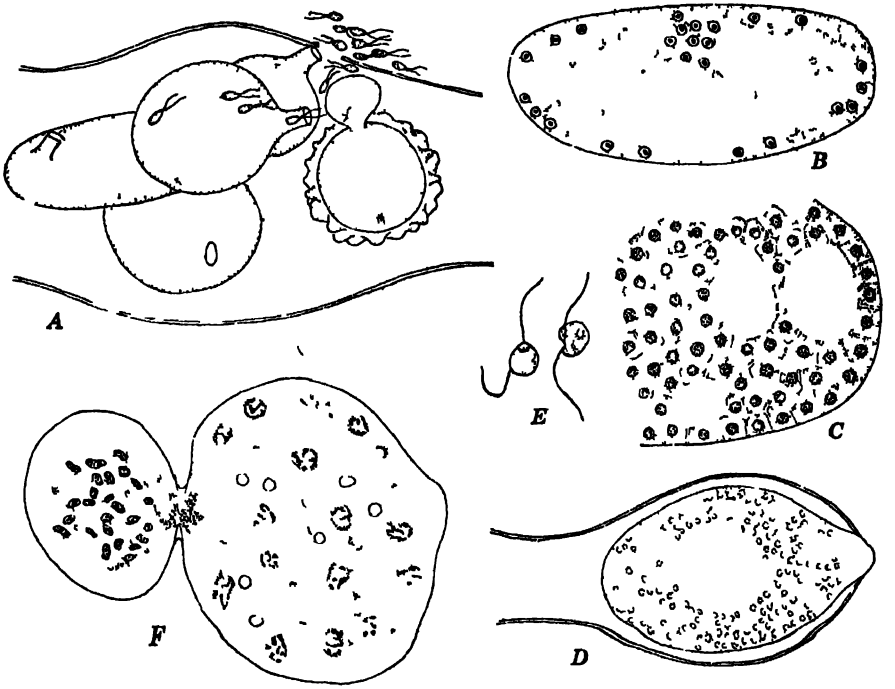


FIG 212.—*A*, sporangia and zygote of *Olpidiopsis Saprolegniae* (Cornu) Fischer *B–F*, *O vexans* Barrett *B–C*, sections of sporangia before and after cleavage of protoplasm *D*, surface view of a sporangium *E* zoospores. *F*, sexual reproduction. (*A*, *after Coker*, 1923, *B F*, *after Barrett*, 1912.)

biflagellate zoospore.[1] The zoospores are liberated through one or more exit tubes that project through the host cell wall. When in the free-swimming condition, a zoospore is broadly ovoid and has the two flagella inserted at or near one pole (Fig. 212*E*). Zoospores that have ceased to swarm come to rest upon the host and secrete a thin wall. The parasite then forms a small pore in the host cell wall, and its protoplast migrates into the host cell.

Instead of producing zoospores the entire mature vegetative plant body may develop into a single multinucleate, nonflagellated gamete.

[1] Barrett, 1912.

Plants developing into male and female gametes lie adjacent to each other. The antheridial plants are surrounded by a wall and have protoplasts containing several nuclei.[1] The oögonial plants are larger, and their protoplasts contain many more nuclei. At the time of fertilization the cell walls disappear in the region of mutual contact, and the protoplast of the antheridium moves into the oögonium (Fig. 212*F*). Sometimes the contents of more than one antheridium moves into an oögonium. The zygote formed by fusion of the two gametes secretes a thick wall that may be smooth or ornamented.[2] The empty antheridium (the *appendicular cell*) remains attached to the zygote for a considerable time. Germination of the zygote has not been observed.

ORDER 2. BLASTOCLADIALES

The Blastocladiales have a true mycelial type of plant body in which the lowermost hyphae are broader than the others. Asexual reproduction is by means of uniflagellate zoospores produced in sporangia formed at the tips of hyphal branches. Sexual reproduction is anisogamous and by a fusion of uniflagellate zoogametes.

The two genera of the order, *Blastocladia* and *Allomyces*, are placed in one family, the Blastocladiaceae. Sexual reproduction has not been observed in any of the seven species of *Blastocladia* but has been found in both species of *Allomyces*.

Allomyces is a saprophyte that is usually found growing on dead insects or other substrata of animal origin. Its mycelium grows erect from a rhizoidal system of delicate hyphal branches. A single stout hypha arises from the rhizoidal system, and it generally has several successive dichotomous branchings (Fig. 213*A*). The branches tend to become progressively smaller at each dichotomy. There is also a complete or incomplete transverse septum at each dichotomy.

Sporangia develop singly or in a catenate succession at the tips of the ultimate dichotomies (Fig. 213*A*). The sporangia of *A. arbuscula* Butler are broadly ovoid. Their development begins with a swelling of the multinucleate tip of a hypha and a formation of a transverse septum that separates the swollen portion from the remainder of the hypha. The number of nuclei increases as the sporangium grows in size.[3] A progressively inward furrowing of the plasma membrane ultimately divides the sporangial contents into uninucleate protoplasts, each of which is then metamorphosed into a uniflagellate zoospore (Fig. 213*C*). The zoospores are liberated through one or more pores developed in the sporangial wall.[4] Instead of dividing into zoospores, the whole protoplast of a sporangium may form a thick special wall internal to the original

[1] Barrett, 1912. [2] Barrett, 1912; Coker, 1923.
[3] Barrett, 1912*A*; Lugg, 1929. [4] Barrett, 1912*A*; Butler, 1911; Coker, 1923.

sporangial wall.[1] This multinucleate akinete or "chlamydospore" (Fig. 213*B*) may be liberated by a breaking of the old sporangial wall.[2] After a rest period of several weeks the chlamydospore germinates by forming a number of zoospores.[3]

Sexual organs are formed at the tips of the ultimate dichotomies of a mycelium but never on one bearing sporangia. The sex organs are

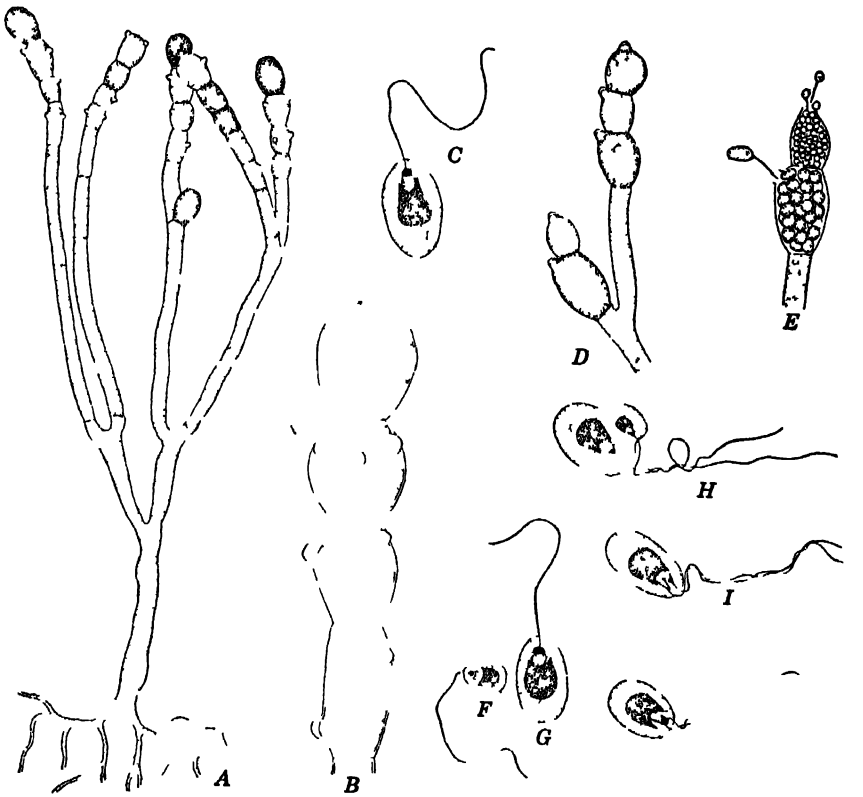


FIG. 213.—*Allomyces javanicus* Kniep. *A*, thallus. *B*, thallus apex with sporangia and an akinete. *C*, zoospore. *D*, young sex organs. *E*, liberation of gametes from sex organs. *F*, male gamete. *G*, female gamete. *H*, gametic union. *I–J*, motile zygotes. (*C–J*, *after Kniep*, 1929.) (*A*, × 120, *B*, × 485.)

borne in short catenate series in which oogonia and antheridia generally alternate with one another on the same branch.[4] The sex organs have the same general shape as sporangia. Antheridia and oogonia may be distinguished from each other by the relative density of their protoplasts (Fig. 213*D*). In *A. arbuscula* the antheridia have denser protoplasts than do the oogonia;[5] in *A. javanicus* the reverse is true.[6] Young multi-

[1] Barrett, 1912*A*; Butler, 1911
[2] Coker, 1923
[3] Barrett, 1912*A*; Kniep, 1930
[4] Hatch, 1933; Kniep, 1929.
[5] Hatch, 1933
[6] Kniep, 1929

nucleate antheridia and oögonia have approximately the same number of nuclei, but the number in an antheridium eventually becomes two to three times that in an oögonium.[1] Gametes are formed by progressive cleavage, and the uniflagellate zoogametes escape singly through one or more pores in the oögonial or antheridial walls (Fig. 213*E*). Free-swimming female zoogametes have a length and breadth more than double that of male zoogametes (Fig. 213*F–J*). Fusion generally takes place while both gametes are motile.[2] The zygote may be biflagellate and continue to swarm for a few minutes, but it soon settles down, and begins germination within an hour.

In *A. javanicus* the mycelium developing from a zygote produces only sporangia or chlamydospores, never gametangia.[3] It is thought that the nuclei of this mycelium are diploid. This opinion[3] is based upon the relative size of the nuclei in asexual and sexual plants rather than upon the actual counts of chromosomes. If this is the case, the life cycle of *A. javanicus* involves an alternation of haploid and diploid generations that are identical in appearance. This alternation is not obligatory since the asexual generation may be reproduced by a formation of diploid zoospores.

ORDER 3. MONOBLEPHARIDALES

The Monoblepharidales have a well-developed mycelium that produces sporangia and sex organs. Asexual reproduction is by means of uniflagellate zoospores. The Monoblepharidales are the only oögamous phycomycetes in which an egg is fertilized by a flagellated antherozoid. They differ from most other mycelial phycomycetes in that the zoospores and antherozoids are uniflagellate.

There is but one family, the Monoblepharidaceae. It contains two genera: *Monoblepharis* with seven species and *Gonapodya* with two. All species are aquatic saprophytes that grow in permanent pools of clear fresh water.[4] They are usually found on dead twigs of various trees, but they have also been found on other substrata.

The mycelium of *Monoblepharis* is usually attached to the substratum by rhizoidal hyphae. According to the species, the remainder of the thallus consists of rigid, sparingly branched hyphae that tend to lie free from one another (Fig. 214*A*) or of freely branched hyphae that lie interwoven in a felted mat. The hyphae are unseptate during vegetative growth. The cytoplasm is alveolate and with a uniseriate row of nuclei that lie equidistant from one another. Reproductive organs are developed at the tips of the hyphae, and the type of organ developed is contingent upon the temperature. If it is 8 to 11°C., reproduction

[1] Hatch, 1933. [2] Hatch, 1933; Kneip, 1929.
[3] Kniep, 1930. [4] Sparrow, 1933.

is asexual; if the temperature is raised to about 20°C., sexual reproduction will follow.[1]

Asexual reproduction (Fig. 214*B–E*) is by means of uniflagellate zoospores produced within a narrowly cylindrical sporangium separated from the remainder of the mycelium by a transverse septum. The protoplast within a sporangium may contain a uniseriate or a multiseriate

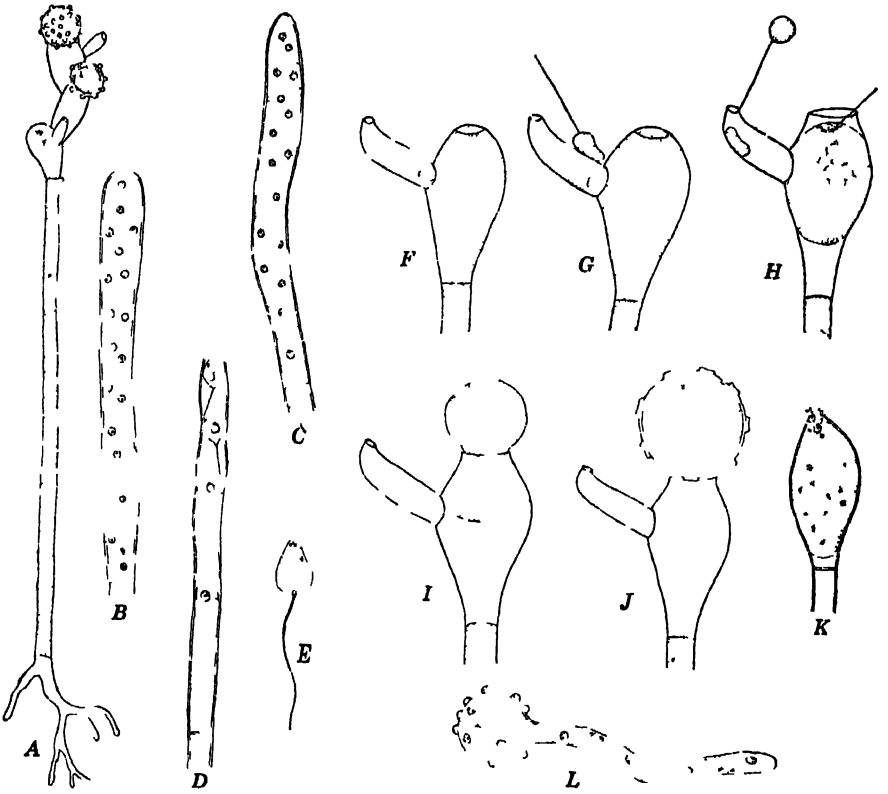


FIG. 214 – *A*, *E J*, *L*, *Monoblepharis polymorpha* Cornu *B–D*, *K M macrandra* (Lag.) Woronin *A*, thallus with mature sex organs *B D*, development of sporangia *E*, zoospore *F J*, diagrams of successive stages in fertilization and development of zygote *K*, union of gametes *L*, germination of zygote (*A*, *E–I*, *after Sparrow*, 1933, *B–D*, *K L after Laibach*, 1927) (*A*, × 185, *B–D*, × 440, *E*, × 630, *F–J*, × 675, *K–L*, × 440.)

row of nuclei.[2] In either case, there is a cleavage of the sporangial contents into angular, uninucleate protoplasts that become metamorphosed into zoospores. A mature sporangium has a circular pore at its apex, and one by one the zoospores creep out through it in an amoeboid fashion. The flagellum of an emerging zoospore remains attached to the pore for some time, and the body of the spore oscillates back and forth. Eventually the spore becomes free and swims about through the water,

[1] Sparrow, 1933 [2] Laibach, 1927.

trailing its flagellum behind it. Upon coming to rest, the zoospore withdraws its flagellum and secretes a wall. When this aplanospore germinates, it generally forms two germ tubes, one growing into the rhizoidal system of the new plant, the other into the remainder of the thallus. In rare cases the entire contents of a sporangium may develop into a chlamydospore.[1]

Development of sex organs is preceded by a formation of several transverse septa in the distal portion of a hypha. These cells alternately mature into antheridia and oögonia. In some species the oögonia lie above the antheridia; in others antheridia lie above the oögonia. Antheridial development, except for the smaller number of uniflagellate swarmers, is similar to that of sporangia. The oögonial protoplast is uninucleate from the beginning,[2] and, during the course of oögonial development, there is a formation of a pore in the apical portion of the oögonial wall.

At the time of fertilization (Fig. 214*F–J*) an antherozoid swims to an oögonium and then crawls, in an amoeboid fashion, over the oögonial wall until it reaches the pore.[3] It then crawls through the pore and fuses with the egg. The resultant zygote may remain within the oögonium or migrate out from the oogonium and remain attached to the pore in the oögonial wall. In either case there is a secretion of a thick zygote wall. The two gamete nuclei do not unite until the zygote wall is formed (Fig. 214*K*), and maturation of the zygote takes several months. During this time there is a reductional division of the fusion nucleus,[2] and each of the four daughter nuclei may divide once or twice. The zygote wall cracks at the time of germination, and the multinucleate protoplast within it sends forth a hyphal outgrowth that is surrounded by a thin wall (Fig. 214*L*).

ORDER 4. ANCYLISTALES

Almost all members of the Ancylistales are parasitic, develop within a single host cell, and have a small, sparingly branched mycelium. At the time of reproduction the mycelium becomes transversely divided into a few cells, each of which develops into a sporangium or into a gametangium. Asexual reproduction is by a formation of biflagellate zoospores. Sexual reproduction is oogamous and by a fusion of aplanogametes. The order includes about 4 genera and 20 species. All of them are placed in a single family, the Ancylistaceae.

Lagenidium is a widely distributed fungus with some 15 species, all but one of them parasitic. Most of the parasitic species grow upon fresh-water algae, but one parasitizes pollen grains and another parasitizes

[1] Sparrow, 1933. [2] Laibach, 1927. [3] Sparrow, 1933; Thaxter, 1895.

the rhizoids of mosses. The single saprophytic species[1] may also be a facultative parasite upon mosquito larvae, *Daphne*, and Copepods.

L Rabenhorstii Zopf grows parasitically within cells of Zygnemataceae, especially *Mougeotia* and *Spirogyra*. Its thallus lies wholly within a single host cell and consists of an irregularly branched hypha (Fig 215*A*). The structure of its protoplast is unknown, but it has been shown[2] that those of certain other Ancylistales are multinucleate. After the cessation of growth, the hypha of *L. Rabenhorstii* becomes transversely divided into several cells, each of which is fertile. In some

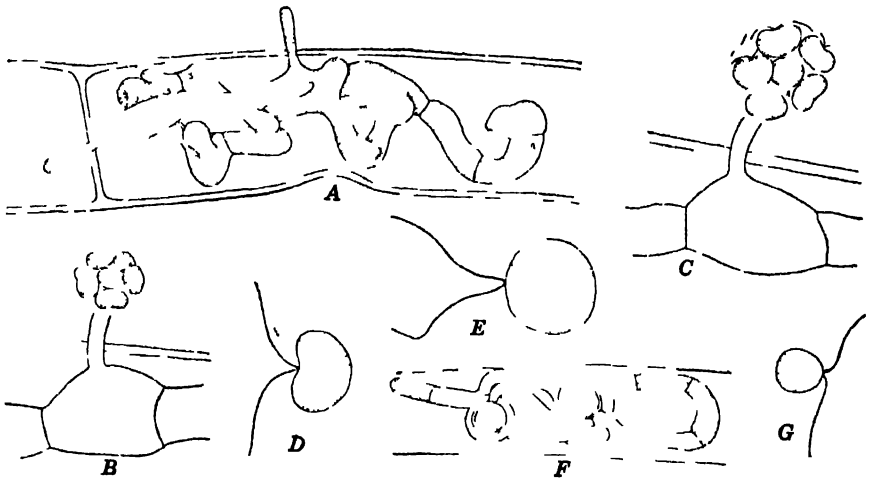


FIG. 215.—*Lagenidium Rabenhorstii* Zopf. *A*, mycelium. *B*, *C*, discharge of sporangial protoplast and formation of zoospores. *D*, zoospore shortly after liberation. *E*, zoospore some time after liberation. *F*, sex organs with zygotes. *G*, zoospore from a germinating zygote. (*After Cook*, 1935.) (*A*, *B*, × 540, *C*, × 790. *D*, *E*, × 1,300, *F*, × 385. *G*, × 790.)

individuals all cells develop into sporangia; in others some cells develop into sporangia and some into sex organs.[3]

There is no evident change in a cell developing into a sporangium other than a formation of a tubular outgrowth, the *exit tube*, that projects through the host cell wall. Formation of the tube is followed by a discharge of the protoplast through it.[3] The globose protoplasmic mass thus liberated remains attached to the tip of the tube and there cleaves into several zoospores (Fig. 215*B–C*). The zoospores are reniform, with two flagella inserted on the concave side. Within a short time they swim away from one another and assume a pyriform shape (Fig. 215*D–E*). Swarming of zoospores may continue for hours or days. At the end of the swarming period, a zoospore comes to rest, with the flagellate end downward, upon a host cell and digests its way directly through the host-cell wall.

[1] Couch, 1935*A*. [2] Dangeard, 1903. [3] Cook, 1935.

At the time of sexual reproduction, the fungus generally develops antheridia and oögonia from adjoining cells of the thallus (Fig. 215*F*). A cell developing into an oögonium becomes rounded, and its protoplast becomes a globose egg that lies some distance in from the oögonial wall. A cell developing into an antheridium remains the same shape and sends forth a slender tubular outgrowth (the *fertilization tube*) that grows through the oögonial wall.[1] The protoplast of the antheridium then migrates through the fertilization tube into the oögonium and there unites with the egg. The zygote formed by this gametic union generally secretes a thick wall. Germination of the zygote to form a single biflagellate zoospore may follow within 24 hours. The protoplast of the host begins to disappear when the sex organs are formed and completely disappears before the zygote germinates. Zoospores liberated from germinating zygotes (Fig. 215*G*) are discharged into the empty host cell and continue swimming about within it until there is a breaking or a disintegration of the host-cell wall.

ORDER 5. SAPROLEGNIALES

The Saprolegniales have a well-developed mycelium in which reproductive organs are developed from the terminal portions of hyphal branches. Asexual reproduction is usually by means of biflagellated zoospores but may be by means of aplanospores. In most cases the spores are formed within sporangia permanently attached to the mycelium, but there are some species of certain genera that form conidiosporangia. Sexual reproduction is oogamous. All of the oogonial protoplasm may go to form eggs, or the peripheral portion of the protoplasm may be cut off in a sterile layer, the *periplasm*. Gametic union is by fusion of a male aplanogamete with an egg that lies within an oögonium. The order includes about 25 genera and 200 species.

As originally delimited from other oögamous phycomycetes, the Saprolegniales included those genera in which all of the protoplasm within an oögonium goes to form one or more eggs. These eggs were thought to develop parthenogenetically.[2] It is now known that parthenogenesis is the exception rather than the rule. Modern cytological methods have also shown[3] that the Saprolegniales intergrade into the oogonial type where the outer portion of the oogonial protoplast is cut off as a sterile layer, the periplasm. Thus, the major, although not the absolute, feature distinguishing the Saprolegniales from other oögamous phycomycetes (with fertilization by means of a male aplanogamete) is the formation of biflagellate zoospores in sporangia that remain permanently attached to the mycelium.

[1] Cook, 1935. [2] DeBary, 1887. [3] Couch, 1932*B*; Kevorkian, 1935.

The Saprolegniales are divided into three families. Ordinarily the Saprolegniaceae and Leptomitaceae are the only families included in the Saprolegniales, and the Pythiaceae are placed in the Peronosporales. Reasons for including the Phythiaceae with the Saprolegniales will be discussed later (page 396).

FAMILY 1. SAPROLEGNIACEAE

The Saprolegniaceae have a mycelium that is not constricted at intervals. The sporangia are generally elongate and only slightly broader than the hyphae bearing them. The protoplasm of a sporangium usually divides to form many biflagellate zoospores; sometimes it divides to form aplanospores, each of which forms a single zoospore. In the development of an oogonium all of the protoplast goes to form one or more eggs. The family includes some 15 genera and 120 species.

The Saprolegniaceae are often known as "water molds," because they are usually found in water and growing saprophytically upon dead bodies of insects, fishes, or upon other animal or plant remains. Some years ago there was a discovery[1] that many, if not all, species also grow in surface soils. It has also been shown[2] that there are Saprolegniaceae which are parasitic on angiosperms.

There are about 25 species in the type genus, *Saprolegnia*. Its mycelium is much-branched, unconstricted, and multinucleate. When individuals of a species are aquatic in habit and growing on dead animal or plant remains, some of the hyphae are short and penetrate the substratum; others are long and extend in all directions from the substratum.

Sporangial development begins with a slight enlargement of the terminal portion of a hypha (Fig 216*A*). After there has been a considerable streaming of cytoplasm and nuclei into the inflated portion, there is a formation of a transverse septum that separates the inflated portion from the remainder of the hypha. Following this there is a progressive cleavage of the multinucleate contents into uninucleate protoplasts (Fig. 216*B*). Cleavage is generally effected by furrows developing from the plasma membrane. The uninucleate protoplasts are metamorphosed into biflagellate zoospores that are liberated through a broad pore developed at the sporangial apex (Fig. 216*C–D*). After escape of the zoospores, the sporangial base may bulge up into the empty sporangium and there develop a new sporangium. This may be repeated three or four times, the successively formed sporangial walls lying nested one within the other.

Free-swimming zoospores are more or less pyriform and have the two flagella at the narrow anterior end. After swimming about for a time, the naked zoospore comes to rest, loses or retracts its flagella,

[1] Harvey, 1925. [2] Jones and Drechsler, 1925; Drechsler, 1927.

assumes a spherical shape, and secretes a wall. This aplanospore stage never germinates directly into a hypha. Instead, its protoplast develops into a single zoospore that escapes through a pore in the wall.

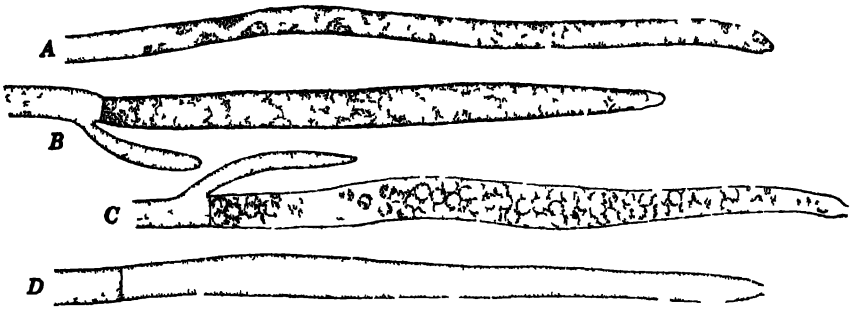


FIG 216.—*Saprolegnia ferax* (Gruith.) Thuret. *A*–*C*, stages in development of sporangia. *D*, empty sporangium. (× 160.)

This zoospore is always reniform and has the two flagella inserted on the concave side.[1] The production of zoospores of two morphological types is called *diplanetism*. In most species when a reniform zoospore ceases swarming it rounds up, secretes a wall, and germinates directly

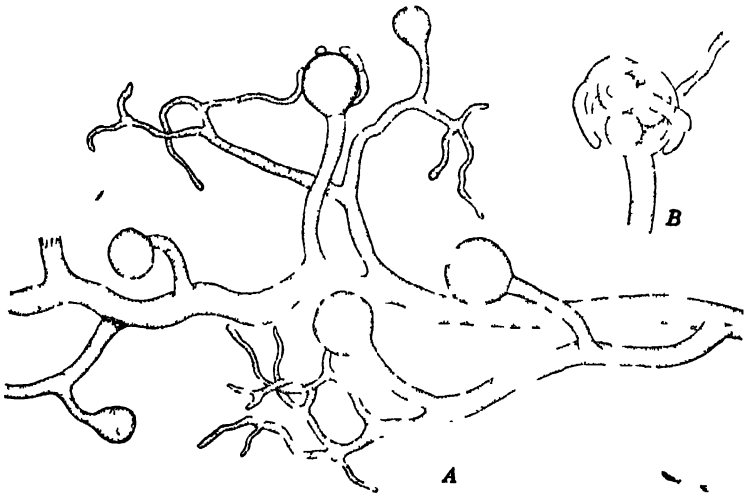


FIG. 217.—*Saprolegnia ferax* (Gruith.) Thuret. *A*, portion of mycelium with young sex organs. *B*, mature sex organs. (× 160.)

into a hypha; but in *S. torulosa* DeBy. it may develop into an aplanospore that germinates to form a second reniform zoospore.[2]

Asexual reproduction may also be effected by a direct formation of spore-like cells from a hypha. These "gemmae" generally lie in a catenate series at the end of a hypha, but they may be intercalary. They are comparable to the oidia formed by many ascomycetes.

[1] Hohnk, 1933; Leitgeb, 1869. [2] Hohnk, 1933.

Sex organs generally develop singly at the tips of hyphae, but sometimes several oogonia develop successively posterior to one another. The sex organs may be borne at the tips of long hyphae or upon short lateral ones. In some species an antheridial and an oogonial branch arise near each other (Fig. 217); in other species they do not. There is a possibility that, as has been shown[1] for a couple of other Saprolegniaceae, that certain of these latter species are heterothallic.

Oogonial development begins with an enlargement of a hyphal tip to form a globose body several times the diameter of the hypha (Fig. 218*A*).

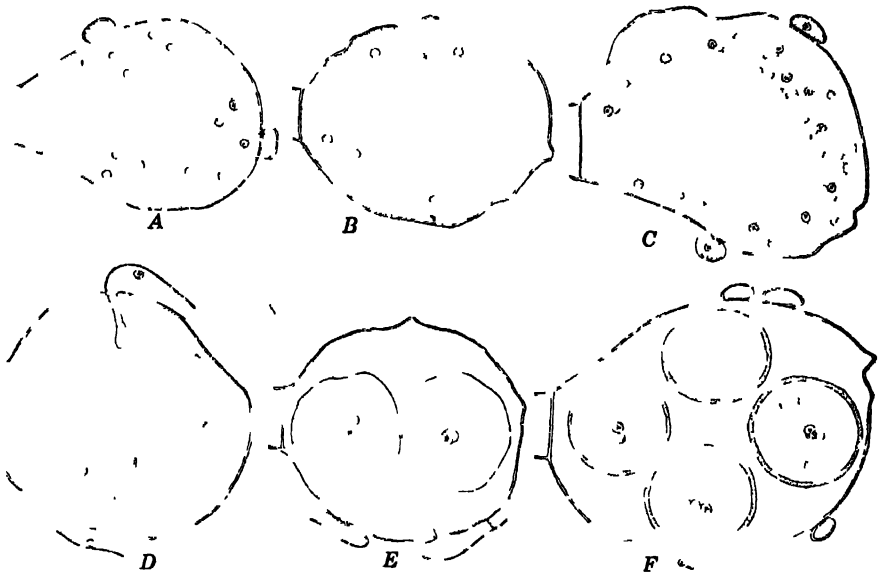


FIG. 218 Development of sex organs of *Saprolegnia* *A*, *B*, oogonia before cleavage of protoplast *C*, the beginning of cleavage *D*, just before fertilization *E*, just after fertilization *F*, ripening zygotes (× 650)

The enlarging oogonium is filled with alveolar cytoplasm and many nuclei that lie equidistant from one another. Sooner or later a transverse septum is formed between the enlarging oogonium and the subtending hypha. As enlargement continues, there is a formation of a large central vacuole within the multinucleate protoplast (Fig. 218*B–C*). Blunt furrows growing centrifugally from the vacuolar membrane eventually cut the protoplasm into a number of fragments each of which may develop into an egg.[2] In most cases the egg is multinucleate when first formed, but there is soon a degeneration of all but one of the nuclei (Fig. 218*D*). The number of eggs within a mature oogonium is variable and ranges from one to 20 in most species.

[1] Coker, 1927; Couch, 1926.

[2] Claussen, 1908; Davis, 1903; Mackel, 1928; Trow, 1895.

The antheridia develop singly at the tips of slender hyphae that have grown toward, and become applied to, developing oögonia. The terminal portion of each of these hyphae enlarges slightly and becomes filled with a nonvacuolate mass of protoplasm in which there are a dozen or so nuclei. Antheridial development terminates with a formation of a cross wall between the inflated portion and the hyphae. In certain species, as *S. ferax* (Gruith.) Thur., no antheridia are developed next to a large percentage of the oögonia. If no antheridia lie next to an oögonium, the eggs within it develop into *parthenospores* that are identical in appearance with zygotes. If there is an antheridium next to the oögonium, it sends out a delicate filamentous outgrowth, the *fertilization tube*, that penetrates the oögonial wall and comes in contact with one or more eggs (Fig. 218*D*). Fertilization is effected by a migration of an antheridial nucleus and possibly some of the cytoplasm into an egg.[1] The two gamete nuclei unite with each other, and the zygote secretes a thick wall (Fig. 218*E–F*).

The zygotes generally ripen for several months before germinating.[2] At the time of germination a zygote may send forth a short hypha and then form several zoospores, or the hypha may develop into a much-branched mycelium.[3] The type of germination is directly dependent upon the amount of available food The scanty cytological observations on germination have been on the type in which there is a short tube.[4] These show that cleavage to form spores may take place before or after outgrowth of the hypha. It is very probable that, as in another genus where germination has been studied more fully,[5] the hypha is more comparable to an exit tube than it is to a sporangium.

FAMILY 2. LEPTOMITACEAE

All of the Leptomitaceae have a mycelium that is constricted at regular intervals and may or may not be differentiated into a stout axis and slender branches. The sporangia are elongate and club-shaped or short and pyriform. In either case they are permanently attached to the thallus and produce many biflagellate zoospores. The sexual reproduction is oögamous and generally, although not always, with a cutting off of periplasm about the single egg in an oogonium. The family includes some 6 genera and 20 species.

Mycelia of the Leptomitaceae may be compared to branching chains of sausages. On this account they are immediately distinguishable from those of other Saprolegniales. Most of the genera[6] delimit a periplasm about the single egg within an oogonium. This is generally given as a

[1] Claussen, 1908; Mäckel, 1928; Trow, 1895. [2] Klebs, 1899; Trow, 1895.
[3] Klebs, 1899. [4] Trow, 1895. [5] Jones and Drechsler, 1925.
[6] King, 1903; Thaxter, 1896; Behrens, 1931; Kevorkian, 1935.

distinctive character of the family and has been considered[1] one of the major reasons justifying establishment of a special order, the Leptomitales. The recent demonstration[2] that there is no formation of periplasm in at least one genus invalidates this generalization.

Both of the two species of *Sapromyces* grow in water and upon dead-plant remains The mycelium has a single basal cell that may or may not be attached to the substratum by a few rhizoids. The basal cell bears two or more erect hyphae at its apex, and each hypha is constricted

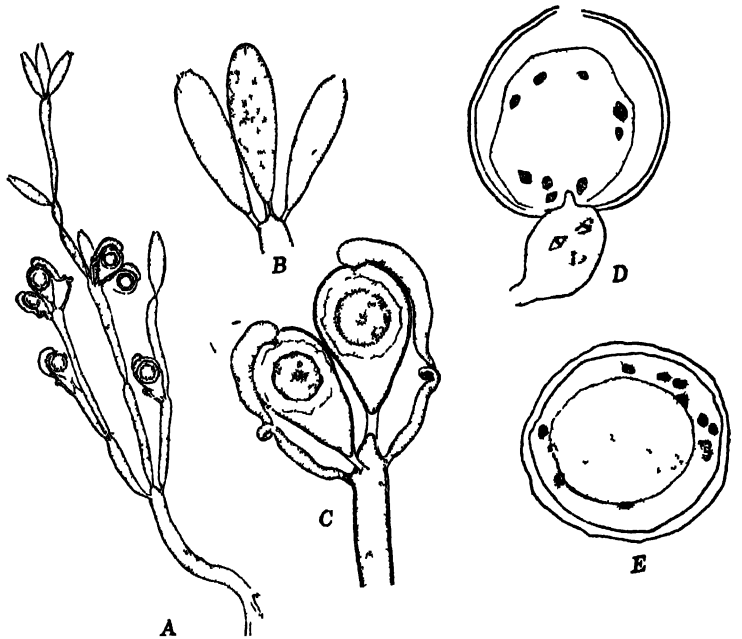


FIG. 219.—*A C*, *Sapromyces androgynus* Thaxter *A*, mycelium with sex organs and sporangia *B*, sporangia *C*, sex organs *D E*, development of sex organs of *S Reinschii* (Schroter) Fritsch (*A–C*, *after Thaxter*, 1896, *D E*, *from Kevorkian*, 1935) (*A*, × 70, *B–C* × 320 *D–E*, × 500)

at its point of origin. The hyphae are repeatedly di- or trichotomously branched and with a constriction at the base of each forking (Fig. 219*A*).

Asexual reproduction is by means of biflagellate zoospores produced within subcylindrical sporangia borne in tufts at the ends of the ultimate branches (Fig. 219*B*). Sporangial development is accompanied by an inflow of cytoplasm and nuclei from the underlying hypha. At first the nuclei are evenly distributed within the sporangium; later on they migrate to the periphery of the cytoplasm as a large central vacuole appears in the center of the protoplast[2] The peripheral cytoplasm then cleaves into uninucleate protoplasts by means of furrows that

[1] Kanouse, 1927 [2] Kevorkian, 1935

develop centrifugally from the vacuolar membrane. Each protoplast is metamorphosed into a reniform biflagellate zoospore in which the flagella are inserted on the concave side, one extending forward, the other backward.

Oogonia and antheridia of *Sapromyces* arise next each other on the tip of the same hypha.[1] A young oogonium contains 10 to 12 nuclei evenly distributed throughout the cytoplasm.[2] These undergo one mitotic division. The cytoplasm soon becomes differentiated into a densely granular peripheral portion and an alveolar central portion (Fig. 219*D–E*). All but one of the nuclei migrate to the peripheral cytoplasm and begin to show signs of disintegration. The nucleus remaining in the alveolar central region enlarges. Sometimes there is a degeneration of all but one nucleus without any preceding outward migration of the other nuclei. In either case there then follows a cytokinesis that cuts off the outer portion (the periplasm) from the central uninucleate portion (the egg).

The antheridial branches[1] are club-shaped and elongate (Fig. 219*C*). Apparently there is no formation of a transverse septum that cuts off the distal portion as a distinct antheridium. There are four to six nuclei in an antheridial branch,[2] and they undergo one mitotic division (Fig. 219*D*). Following this, one of them enlarges, and the others degenerate. At the time of gametic union the antheridial branch sends forth a fertilization tube that pushes through the oogonial wall and to the egg. This is followed by a migration of the male nucleus into the egg and a fusion of it with the egg nucleus. The zygote is known to develop a thick wall but its germination has not been observed.

FAMILY 3. PYTHIACEAE

The Pythiaceae have a well-developed mycelium that is without constrictions at intervals. Asexual reproduction is by means of biflagellate zoospores that are formed within sporangia which either remain permanently attached to the mycelium or become detachable condidiosporangia. Sometimes the conidiosporangia germinate directly into hyphae. Sexual reproduction is oogamous and with a cutting off of a periplasmic layer about the single egg within an oogonium. The family includes about five genera and 45 species.

The Pythiaceae are a connecting link between the Saprolegniales and the Peronosporales. Their various characters are so intermediate that some[3] refer them to the Peronosporales and others[4] refer them to the Saprolegniales. One reason for placing them among the Peronosporales is the regular formation of a periplasm about the egg. However,

[1] Thaxter, 1896. [2] Kevorkian, 1935.
[3] DeBary, 1887 [4] Schroter, 1892–1893.

this is not unique for the Peronosporales since it is quite general among the Leptomitaceae, a family that obviously belongs to the Saprolegniales. Another argument given for referring the Pythiaceae to the Peronosporales is their ability to form conidiosporangia. In all genera of Pythiaceae certain species produce conidiosporangia, and others regularly have the sporangia remaining attached to the mycelium. Since the majority of Pythiaceae form sporangia instead of conidiosporangia, it is probably better to refer the family to the Saprolegniales.

Pythium is a genus with about 40 species [1] A few species are true aquatics and parasitic upon various fresh-water algae, but many more grow in soil Many, if not all, of the species that grow saprophytically

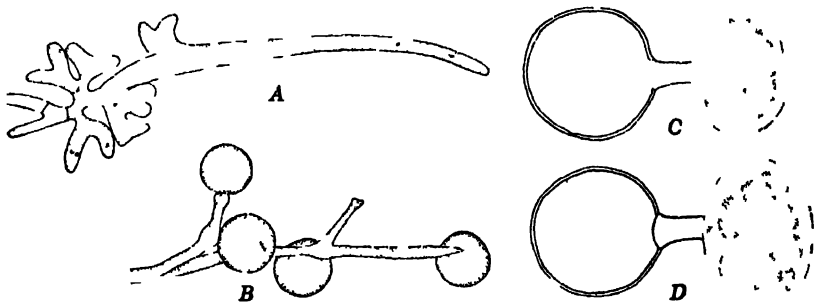


FIG. 220.—*A* Sporangium of *Pythium aphanidermatum* (Edson) Fitzpatrick *B–D*, *P intermedium* DeBary *B*, conidiosporangia *C D* discharge of conidiosporangial contents and formation of zoospores (*A*, *after Edson*, 1915, *B D*, *after Atkinson*, 1895) (*A*, × 125, *B*, × 550, *C D*, × 1,100)

in soil can also infect the roots of various land plants and there continue growth as parasites Infection generally takes place at the seedling stage of the development of the host, and *Pythium* often produces a wide-spread "damping off" of seedlings in greenhouses, cold frames, and seedbeds The freely branched mycelium of *Pythium* does not have certain of the hyphae differentiated into rhizoids as do mycelia of Saprolegniaceae. Young mycelia are unseptate, but old ones may develop transverse septa [2] When the fungus is parasitic, some of the hyphae may be within and others outside of the host; or all may lie within it.

Asexual reproduction is generally by means of biflagellate zoospores. These may be formed in sporangia that remain attached to the mycelium or in detachable conidiosporangia. Sometimes asexual reproduction is effected by a direct germination of conidiosporangia or, as in certain Saprolegniaceae, by gemmae.

The sporangia are of two types; elongate sporangia that are of the same diameter as the hyphae bearing them and those that are globose and much broader than the hyphae. Sporangia of the first type are

[1] Matthews, 1931 [2] Butler, 1907.

always formed toward the end of a hypha. The portion developing into a sporangium may be unbranched or have several irregularly twisted lateral branches (Fig. 220*A*). In certain species the sporangial portion is set off from the remainder of the mycelium by a transverse wall;[1] in others it is not.[2] The method of zoospore formation is variable, even in the same species. Some individuals of *P. aphanidermatium* (Edson) Fitzpatrick have a progressive cleavage of the sporangial contents into uninucleate protoplasts that metamorphose into biflagellate zoospores.[1] The mass of spores thus formed lies within a delicate wall distinct from the sporangial wall. A larger number of individuals of *P. aphanidermatium* have the protoplast within a sporangium remaining undivided and becoming surrounded by a special wall. The protoplast, surrounded by a special wall, then moves out through a break in the sporangial wall. In such a case, cleavage and metamorphosis into zoospores follow immediately after emergence.[1] The membrane surrounding the mass of zoospores persists for a short time only. After it disappears, the zoospores swim freely in all directions.

Globose sporangia generally develop at the ends of hyphae, but the apex of a sporangium may proliferate a hypha and the sporangia thus become intercalary.[3] Globose sporangia have transverse walls between them and the hyphae on which they develop (Fig. 220*B*). These sporangia generally have an evident exit tube, and they always discharge their protoplasts before cleavage. The discharged protoplasts are always surrounded by a thin wall that persists until after the zoospores are formed (Fig. 220*C–D*). Some species develop detachable globose sporangia. Such conidiosporangia may germinate directly, or they may have a division of their contents into zoospores. Sometimes sporangia and conidiosporangia have their protoplasts secreting a thick wall and becoming chlamydospores that generally remain dormant for several weeks. A germinating chlamydospore may form zoospores, or it may send forth a hypha that grows directly into a mycelium.

At the end of the swarming period, a zoospore assumes a spherical shape and secretes a wall. In most cases this cell germinates by sending forth a hypha, but it may germinate to form a single zoospore.[4] The production of a second zoospore resembles the diplanetism of *Saprolegnia* but is not strictly comparable to it because the newly formed zoospore is similar to the original one.

Oögonial development begins with a globose enlargement of a hyphal tip and a migration of nuclei and cytoplasm into the enlarging portion (Fig. 221*A*). Soon after this there is a formation of a transverse wall setting off the inflated portion, the oögonium. The number of nuclei

[1] Edson, 1915. [2] Butler, 1907.
[3] Hohnk, 1932; Kanouse and Humphrey, 1928. [4] Höhnk, 1932.

within an oögonium may[1] or may not[2] be increased by division. In either case all but one of them migrate to just within the plasma membrane and lie within the periplasm cut off at the peripheral portion of the oögonial protoplast. The antheridia develop at the tips of hyphae that lie against the oögonium. These hyphae become slightly inflated at the distal end and form a cross wall back of the inflated portion. The cell thus formed is the antheridium. In *P. aphanidermatium* all but one of the antheridial nuclei degenerate. In this species there is a formation of a wide pore where oögonial and antheridial walls adjoin. Establishment of

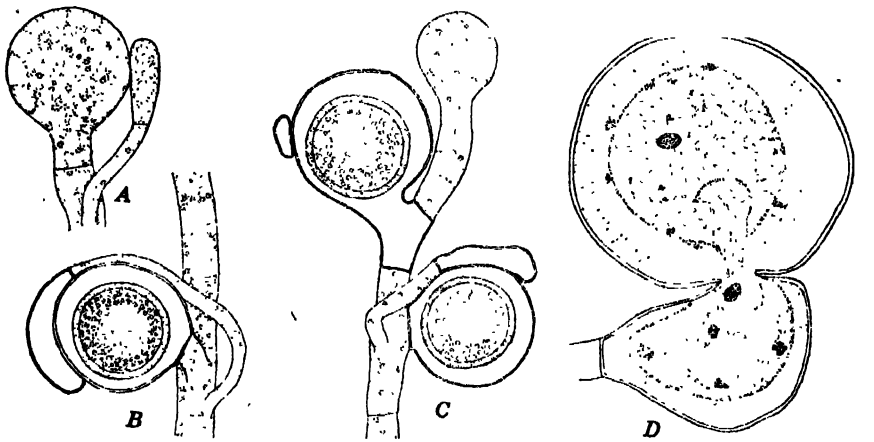


FIG. 221.—*A–C*, development of sex organs of *Pythium intermedium* DeBary. *D*, gametic union in *P. aphanidermatium* (Edson) Fitzpatrick. (*D*, *after Edson*, 1915.) (*A–C*, × 650; *D*. × 1,500.)

the pore is followed[2] by a migration of the antheridial nucleus and a considerable amount of cytoplasm through the periplasm and into the egg (Fig. 221*D*). Other species have the antheridium forming an evident fertilization tube that pushes through oögonial wall and periplasm to the egg.

The zygote secretes a thick wall (Fig. 221*B–C*), and the two gamete nuclei unite. The fusion nucleus divides into several daughter nuclei before germination,[3] and it is very probable that the first division is reductional. Germination of the zygote is direct and into a hypha.

ORDER 6. PERONOSPORALES

All Peronosporales are parasites that grow on land plants. The thallus is a well-developed mycelium producing conidiosporangia and sex organs. Germinating conidiosporangia may either form a number of biflagellate zoospores or may develop directly into mycelia. Sexual reproduction is oögamous and with a delimitation of periplasm about the

[1] Miyake, 1901; Trow, 1901. [2] Edson, 1915. [3] Trow, 1901; Edson, 1915.

single egg within an oögonium. Fertilization is by union of a male aplanogamete with the egg.

The order contains some 8 genera and 280 species. It is divided into two families.

FAMILY 1. PERONOSPORACEAE

The Peronosporaceae include all Peronosporales that have a branching sporangiophore projecting beyond the host. All sporangiophores bear conidiosporangia singly at the tips of their ultimate branches. The family contains about 7 genera and 250 species. These are often called the "downy mildews."

About 190 species of *Plasmopara* have been described, but many of them are morphologically indistinguishable and differ only in the hosts they infect. From the economic standpoint, the most important species is *P. viticola* (B. & C.) Berl. & DeT., a parasite of the grape and one that caused serious damage to vineyards before methods of control were discovered.

The downy mildew of grapes grows as an intercellular parasite within leaves and young stems. The mycelium is multinucleate, freely branched, and with the branches varying greatly in size. The hyphae bear numerous globose lateral outgrowths (*haustoria*) that penetrate walls of the host cells and absorb food from their protoplasts.

After it is well established within the host, the mycelium forms dense masses of branches in the cavities beneath stomata of the host. Several of these hyphal branches grow out through a single stoma and develop into sporangiophores. Each sporangiophore has three to six fairly long lateral branches borne in monopodial succession (Fig. 222*A*). The lateral branches lie more or less at right angles to the main axis and each bears several short branchlets. A single conidiosporangium is formed at the tip of each branchlet, and it is readily detachable from the narrow branch tip (*sterigma*) immediately below. A detached conidiosporangium usually forms several zoospores when it germinates (Fig. 222*C–F*), but it may also germinate directly into a mycelium.[1]

Development of conidiosporangia has been most thoroughly studied in *P. Halstedii* (Farl.) Berl. & DeT. A very young conidiosporangium of *P. Halstedii* is uninucleate, but this nucleus divides and redivides as the conidiosporangium increases in size. At the cessation of nuclear division the nuclei are spherical and equidistant from one another. Shortly afterward they become pyriform (Fig. 222*B*), migrate to just within the plasma membrane, and come to rest with the narrow end facing outward. There then follows an inward furrowing of the plasma membrane that cuts the protoplasm into uninucleate protoplasts, each of which metamorphoses

[1] Gregory, 1912

into a biflagellate zoospore. The zoospores are fully mature at the time a conidiosporangium is shed, and germination may follow within an hour. A germinating conidiosporangium develops a circular pore in the distal end of the enclosing wall, and the zoospores escape through the pore. Free-swimming zoospores of *P viticola* are reniform and with the two flagella inserted on the concave side (Fig 222*G*) One flagellum extends forward, the other backward.[1] After swarming for a half hour or so, the

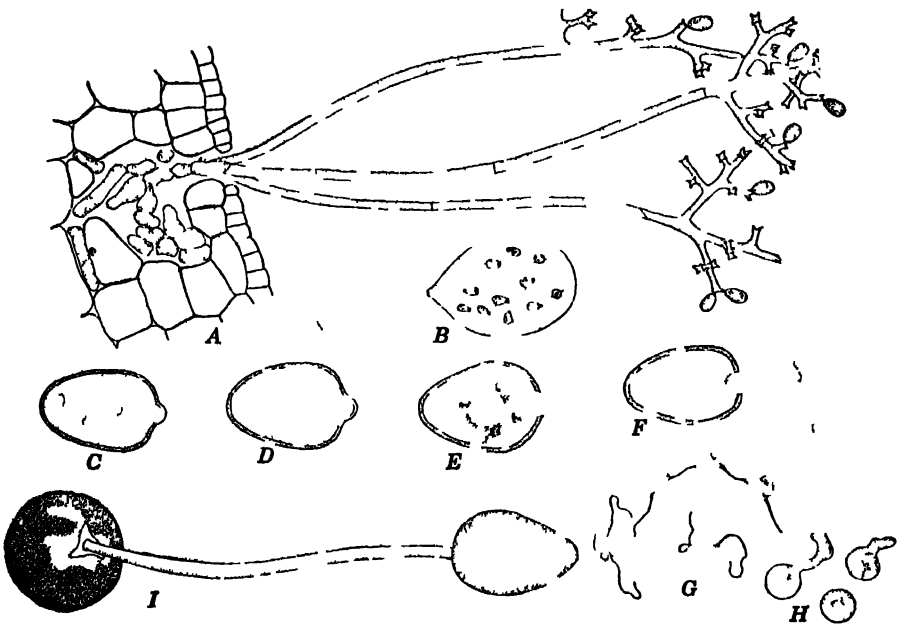


FIG 222.—*Plasmopara viticola* (Berk and Curt.) Berl and De Toni. *A*, sporangiophore *B*, multinucleate conidiosporangium *C–F*, germination of conidiosporangium *G*, zoospores *H* germination of zoospores *I* germination of zygote (*C–H after Gregory*, 1912, *I*, *after Atkins*, 1929) (*A* × 160, *B*, × 975)

zoospore comes to rest, rounds up, and secretes a thin wall (Fig 222*H*). When a conidiosporangium has germinated upon a leaf, the zoospores show a marked tendency to come to rest in the immediate vicinity of stomata The globose cell formed from the zoospore soon sends out a germ tube that grows directly through a stoma [1]

Development of sex organs is essentially the same in all three species where it has been investigated.[2] The sex organs are formed within tissues of the host and at the tips of hyphae. The hyphal tip developing into an oogonium enlarges greatly and contains many nuclei that lie approximately equidistant from one another. After formation of a

[1] Gregory, 1912 [2] Nishimura, 1926; Rosenberg, 1903; Ruhland, 1903.

transverse wall separating the oögonium from the subtending hypha, all but one of the oögonial nuclei accumulate in a layer some distance in from the plasma membrane. Sometimes the nuclei divide after they have come to lie in this layer. Sooner or later there is a cytokinesis that divides the oögonial protoplast into a central uninucleate egg and a peripheral multinucleate periplasm. Meanwhile, a hyphal tip lying against the oögonium has developed into an antheridium by forming a cross wall that separates off an antheridial protoplast containing about a dozen nuclei. The antheridium sends forth a fertilization tube that grows through the oögonial wall, through the periplasm, and into the cytoplasm of the egg. Discharge of a male gamete nucleus into the egg is followed by a secretion of a thick wall about the zygote.

Germination of the zygote of *P. viticola* does not take place until the next spring. Union of the two gamete nuclei is also often delayed until the next spring,[1] but, when it does take place, there is an almost immediate division and redivision of the fusion nucleus into 60 or more daughter nuclei. The first division of this series is thought to be reductional. The zygote sends out a germ tube shortly after nuclear division ceases, and, if the zygote lies in old dead leaf, this then grows through a stoma. The multinucleate protoplast within the zygote wall migrates into the distal end of the tube and a cross wall is laid down. The portion thus cut off at the tip of a germ tube then develops into a sporangium containing 60 or more zoospores that are liberated through a pore in the sporangial apex.[2]

FAMILY 2. ALBUGINACEAE

The Albuginaceae have unbranched sporangiophores that lie in a palisade-like layer beneath the epidermis of the host. Each sporangiophore cuts off a succession of conidiosporangia at its apex. There is but one genus, *Albugo*. It includes some 25 species.

A. candida (Pers.) Kuntze, parasitic on several crucifers, is one of the species that was first thought to belong to *Uredo*, a form genus of the rusts. Because of its color it was called the "white rust," and this name has remained in common usage ever since. The white rust may infect stems, leaves, flowers, or fruits of the host. Its mycelium is multinucleate, generally unseptate, and with numerous branches that grow between the host cells. The hyphae bear numerous globose haustoria that penetrate walls of the host cells and absorb food from their protoplasts. After growing throughout tissues adjoining the point of infection, the fungus produces a dense mat of hyphae just beneath the epidermis of the host. Numerous short erect hyphae (sporangiophores) grow erect from

[1] Arens, 1929. [2] Arens, 1929; Gregory, 1912.

the mat (Fig. 223*A*). The protoplast within a sporangiophore contains about a dozen nuclei. The distal portion of a sporangiophore is enclosed by a thin wall; the lower portion is surrounded by a greatly thickened wall. The upper end of a sporangiophore enlarges slightly and is then cut off as a five- to eight-nucleate conidiosporangium by the formation of a transverse wall. The portion of the sporangiophore just beneath the conidiosporangium soon enlarges and becomes cut off as a second conidiosporangium. This may be repeated indefinitely. The accumulating

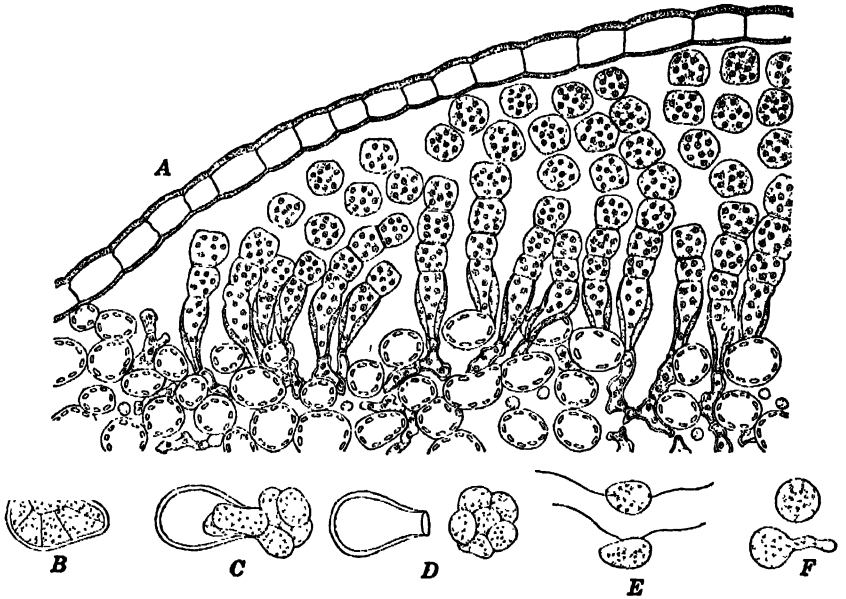


FIG. 223.— *Albugo candida* (Pers.) Kuntze. *A*, development of conidiosporangia beneath epidermis of host. *B–D*, germination of conidiosporangia. *E*, zoospores. *F*, germination of zoospores. (*B–F*, *after DeBary*, 1863.) (*A*, × 325; *B–F*, × 400.)

mass of conidiosporangia pushes out and eventually bursts the overlying epidermis. These exposed conidiosporangia are the white, mealy patches evident on the host. Division of the conidiosporangial protoplast into zoospores and their subsequent liberation take place within 2 to 10 hours after they are shed (Fig. 223*B–D*). The optimum temperature for germination is around 10°C.[1] The zoospores are reniform and with two flagella (Fig. 223*E*) inserted on the concave side. Sometimes[2] there is a direct germination without a production of zoospores. Zoospores that have ceased to swarm become spherical, secrete a wall, and send out a hypha (Fig. 223*F*) that grows through a stoma of the host.[3]

Toward the end of the growing season of the host, certain of the hyphae penetrate the deeper lying tissues of stem or petiole and there

[1] Melhus, 1911. [2] Palm, 1932. [3] DeBary, 1863.

form sex organs. In *A. candida*[1] an inflated hyphal tip developing into an oögonium forms a cross wall just below the inflation. At first the cytoplasm within the young oogonium is uniformly vacuolate and with the nuclei evenly distributed (Fig. 224*A*). Later on, the central portion of the cytoplasm becomes denser, and all nuclei migrate to the periphery of it. Here the nuclei divide mitotically, and many of the spindles are so oriented that one daughter nucleus lies within the dense central cytoplasm and the other within the more vacuolate outer cytoplasm (Fig. 224*B*).

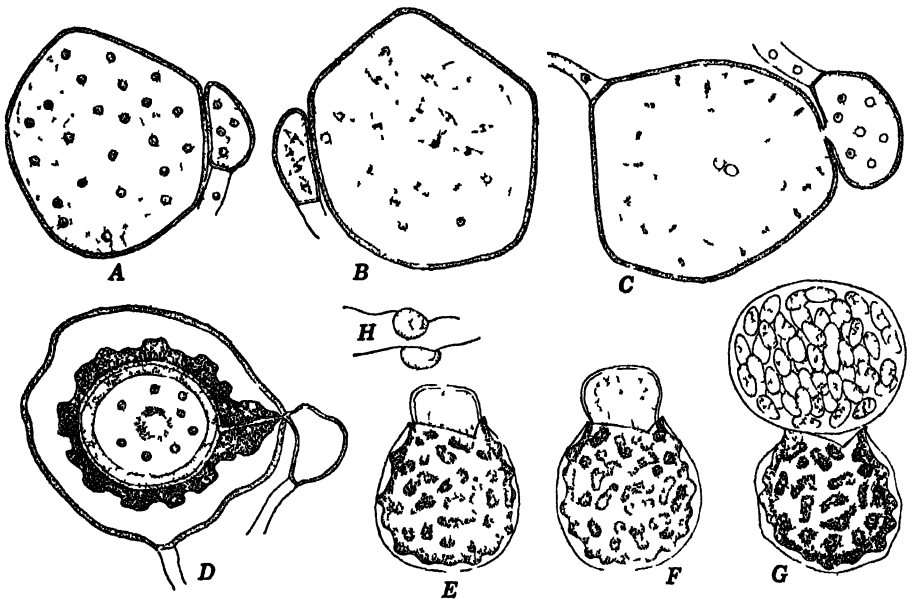


FIG. 224.—Sexual reproduction of *Albugo candida* (Pers.) Kuntze. *A*, oogonium before differentiation of egg. *B*, at the beginning of differentiation of egg. *C*, after fertilization. *D*, old zygote. *E*, *G*, germination of the zygote. *H*, zoospores from a germinating zygote. (*E–H*, *after DeBary*, 1863.) (*A–D*, × 650, *E*, *H*, × 400.)

There then follows a cytokinesis that divides the dense and vacuolate portions into egg and periplasm. An egg contains several nuclei when first delimited, but all but one of them soon disintegrate. In certain other species of *Albugo*,[2] the multinucleate egg has no degeneration of nuclei. Meanwhile, tips of other hyphae lying against the oogonium have formed cross walls that cut off small antheridia, each containing a few nuclei. The antheridium of *A. candida* forms a slender fertilization tube that grows through the oogonial wall, through the periplasm, and penetrates rather deeply into the egg (Fig. 224*C*). A male gamete nucleus then enters the egg and fuses with its nucleus. In the species with multinucleate eggs, several male nuclei enter an egg and each unites with an egg nucleus.

[1] Davis, 1900; Stevens, 1901; Wager, 1896. [2] Stevens, 1899, 1901.

The zygote of *A. candida* soon secretes a thick wall with three distinct layers (Fig. 224*D*). The fusion nucleus divides within a relatively short time and the two daughter nuclei divide. The four nuclei divide into eight, and simultaneous division continues until there are 32 nuclei.[1] The zygote usually overwinters in the 32-nucleate stage. When it germinates the next spring, there is a formation of more than 100 biflagellate zoospores.[2] The zygote wall then cracks, and the zoospores are extruded in a mass that is surrounded by a thin vesicle (Fig. 224*E–H*). This soon disappears, and the zoospores swim freely in all directions.

ORDER 7. MUCORALES

The Mucorales (black molds) have a well-developed, freely branched mycelium that is generally without transverse septa in the vegetative portion. Asexual reproduction is by means of aplanospores that are formed within sporangia. Sexual reproduction is isogamous, or approximately so, and by fusion of the two multinucleate aplanogametes within two apposed gametangia.

The order includes about 25 genera and 400 species. These have been divided[3] into seven families differing from one another in structure of the sporangium. A majority of the species are saprophytic, a few are parasitic on other fungi, and some cause diseases of animals or plants.

Rhizopus is a genus with about 35 species. One of these, *R. nigricans* Ehr. is so widely distributed that it is often called the weed of laboratory cultures. A young mycelium of *R. nigricans* is multinucleate, is unseptate, and has all the hyphae alike. Later on the mycelium becomes differentiated into hyphae of three types: repeatedly branched rhizoids that penetrate the substratum; *stolons* that grow horizontally above the substratum for some distance and then bend down to the substratum and form a tuft of rhizoids; and the vertically erect *sporangiophores* that grow in tufts where the stolons form rhizoids (Fig. 225).

A sporangiophore is unbranched. After it has elongated to a certain height, its tip begins to enlarge into a sporangium. Cytoplasm, many nuclei, and a considerable amount of reserve food flow into the enlarging sporangium (Fig. 226*A*). Most of the protoplasm accumulates in a thick layer just inside the enlarging sporangial wall, leaving the center occupied by a vacuolate protoplasm in which there are a few nuclei. A dome-shaped layer of vacuoles then appears between the dense and the vacuolate portions of the protoplasm. These vacuoles flatten and fuse laterally with one another to form a dome-shaped cleft between the two portions of the protoplasm (Fig. 226*B*). An inward furrowing of the plasma membrane at the base of the sporangium completes the cleft between the two portions. There is next a secretion of a wall between the recently

[1] Wager, 1896 [2] DeBary, 1863. [3] Fitzpatrick, 1930.

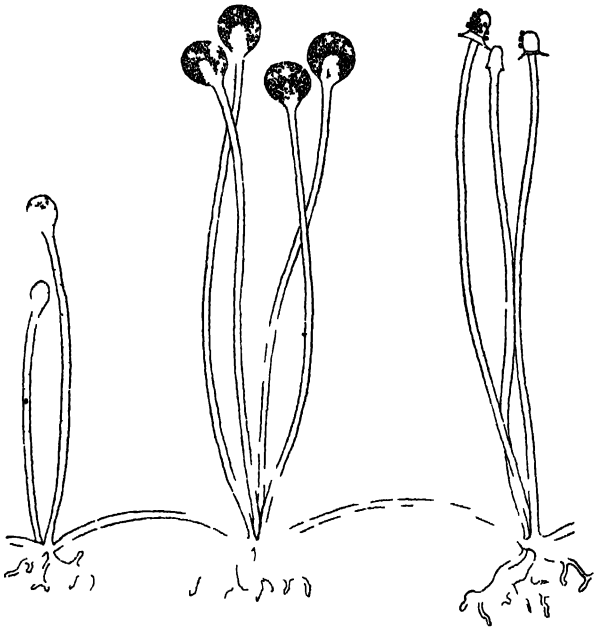


FIG 225.—Portion of a fruiting mycelium of *Rhizopus nigricans* Ehr (diagrammatic) (× 30)

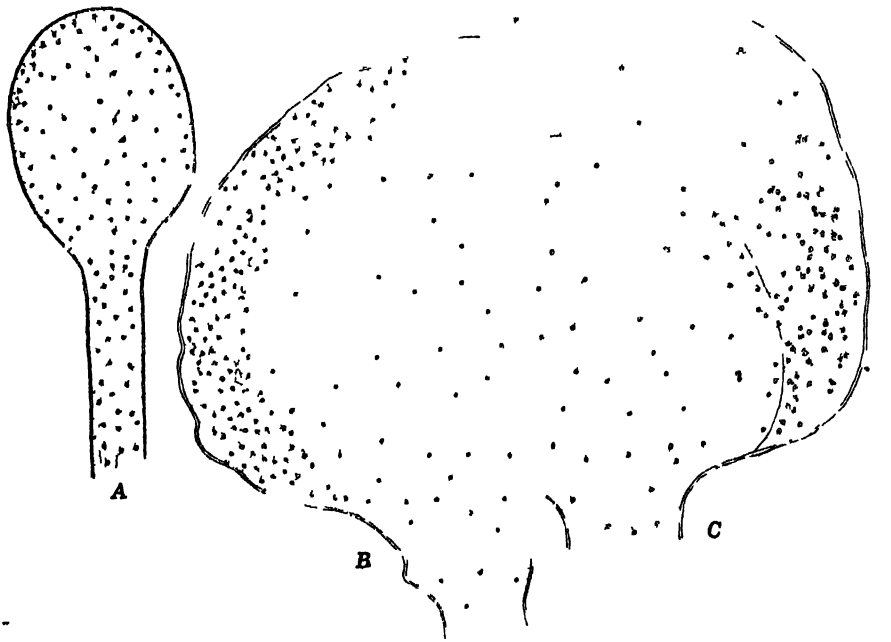


FIG 226.—Stages in the development of sporangia of *Rhizopus nigricans* Ehr *A* before formation of columella *B* during formation of columella *C* during spore formation by progressive cleavage (× 325)

divided protoplasts. This completely separates the dome-shaped sterile portion (the *columella*) of a sporangium from the outer fertile portion.[1] The plasma membrane of the protoplast within a fertile portion next develops numerous branching inwardly growing furrows (Fig. 226*C*). These divide the protoplasm into smaller and smaller fragments. With continuation of this progressive cleavage, there is ultimately a division of the fertile protoplasm into irregularly shaped protoplasts each with 2 to 10 nuclei. The protoplasts then round up, secrete walls, and become aplanospores. The sporangial wall dries out after the aplanospores are

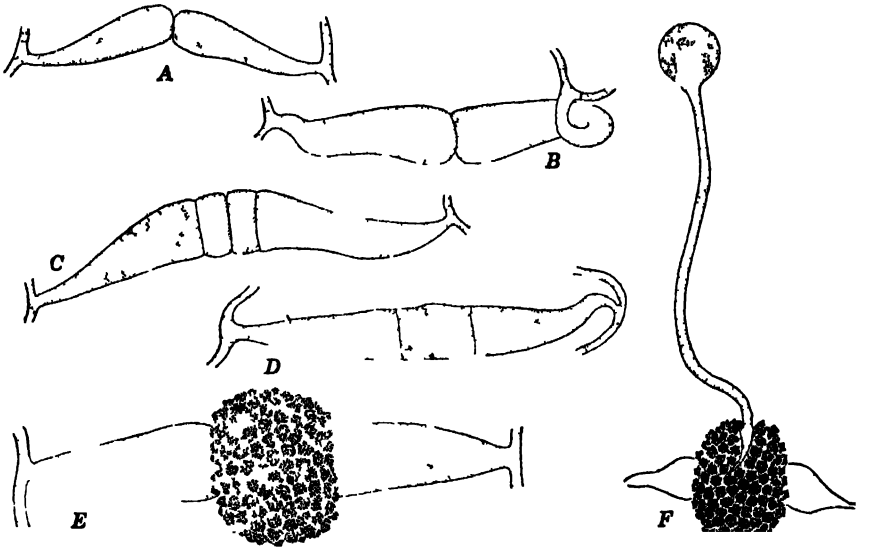


FIG. 227.—Sexual reproduction of *Rhizopus nigricans* Ehr. *A–B*, progametangia. *C*, after the formation of gametes. *D E* young and mature zygotes. *F*, germination of a zygote (diagrammatic). (*A E* × 160. *F* × 80.)

mature and is so fragile that any slight disturbance ruptures it. The stalk of a sporangiophore and the columella persist after liberation of the spores by rupture of the sporangial wall.

Rhizopus may also reproduce asexually by means of chlamydospores. These are rarely, if ever, formed in *R. nigricans*, but they are of frequent occurrence in certain other species.[2] They are produced in old mycelia that have become transversely septate and are due to a thickening of walls in certain intercalary cells.

R. nigricans is heterothallic,[3] and there is no sexual reproduction unless hyphae of two different sexes come in contact with each other. When this does take place, zygotes are formed in abundance. When hyphae of two sexes meet, each may produce a short side branch (*progametangium*) at the point of contact (Fig. 227*A*). The distal portion of each pro-

[1] Swingle, 1903. [2] Lendner, 1908. [3] Blakeslee, 1904.

gametangium becomes inflated and densely filled with protoplasm (Fig. 227*B*). Each progametangium forms a transverse wall that divides it into a distal cell (the *gametangium*) that contains a densely granular multinucleate protoplast and a proximal cell (the *suspensor*) that contains a more vacuolate multinucleate protoplast (Fig. 227*C*). There is considerable variation in size between the two gametangia in the various pairs formed when two mycelia interlock. In some pairs the two gametangia are equal in size; in others they are markedly unequal. After each gametangium of a pair has increased in size and the number of its nuclei has increased, there is a development of a large pore where the two gametangial walls abut on each other. The two gametangial protoplasts then intermingle with each other to form a zygote that soon becomes surrounded by a thick, black, warty wall (Fig. 227*D–E*). The behavior of the gamete nuclei is uncertain. A fusion of a majority of them in pairs has been described for *R. nigricans*[1] and for certain other genera of Mucorales.[2] Others who have studied the development of zygotes in *R. nigricans* and other Mucorales hold that there is no nuclear fusion.[3]

After a considerable period of rest, the zygote of *R. nigricans* germinates by sending forth a short, very sparingly branched hypha in which a sporangium develops at the apex of one branch (Fig. 227*F*). Aplanospore formation within this sporangium is similar to that in sporangia borne on vegetative mycelia. Nothing is known concerning the segregation of heterothallic strains during zygote germination in *R. nigricans*. In certain other heterothallic Mucorales it has been shown[4] that in a sporangium produced after zygote germination some genera have all spores the same sex and other genera have some spores of one sex and some the other.

ORDER 8. ENTOMOPHTHORALES

Among the Entomophthorales the thallus ranges from one that is nonhyphal in the vegetative condition to one that is a profusely branched mycelium. Species with a hyphal mycelium have an early septation of it into cells with a few nuclei each. Asexual reproduction is by the development of conidiosporangia that germinate directly. With one or two exceptions, the conidiosporangia are violently discharged from the underlying sporangiophore. Sexual reproduction is by the apposition of two gametangia and the fusion of two aplanogametes of equal or unequal size.

The order includes about 7 genera and 60 species; some saprophytic; others parasitic on insects. Some mycologists place all of the 50 or more entomogenous species in a single genus, variously called *Empusa* or *Entomophthora*. Other mycologists range the entomogenous parasites in three genera, one without and two with a violent discharge of conidio-

[1] Moreau, 1913. [2] Keene, 1914, 1919. [3] Baird, 1924. [4] Blakeslee, 1906.

sporangia. According to this treatment, the entomogenous species with a multinucleate conidiosporangium borne on an unbranched sporangiophore are assigned to *Empusa*, and those with a branched sporangiophore bearing uninucleate conidiosporangia to *Entomophthora*.

If one follows the second usage described above, the genus *Empusa* comprises about a dozen species. The commonest of these is *E. Muscae* Cohn, a parasite of the common house fly. House flies infected with *Empusa* are most abundant in late summer and early autumn. Experiments[1] show that the fungus usually develops to maturity within five to eight days after a fly is infected. Infected flies may be recognized by their sluggishness, lightening in color of the abdomen, and the peculiar dirty brick-red color of the eyes.[2] Flies dying from effects of the fungus crawl slowly over the ceiling or high on the side walls of a room. At the time of death they are firmly affixed by their proboscides to the object over which they were crawling. Here they remain after death, and the fungus develops conidiosporangia that shoot from the sporangiophores at maturity. These discharged conidiosporangia are the smoky halo that one sees beneath flies that have died on window panes or on mirrors.

During the early stages of vegetative development within a house fly, *E. Muscae* consists of small, globose, multinucleate *hyphal bodies*. These multiply rapidly. In another species of *Empusa* the hyphal bodies are regularly four-nucleate and reproduce by transverse constriction after the nuclei have divided into two groups of four daughter nuclei each.[3] Among certain species, including *E. Muscae*, the vegetative stage consists entirely of hyphal bodies. In certain other species there is a development of a true vegetative mycelium. The mycelium of one of these species has been grown in artificial culture.[4] The hyphal bodies become distributed throughout the body of the host, and it is thought[5] that their dispersal is due to a transporation in the blood stream. Multiplication of hyphal bodies continues until they have replaced most of the tissues within the integument of a fly.

Shortly before the death of the host, each hyphal body of *E. Muscae* sends forth an unbranched tubular outgrowth, the immature sporangiophore, that grows toward the chitinous integument covering the abdomen of the fly (Fig. 228*B*). The elongating sporangiophores lie in tufts that push through the thin places between segments of the integument (Fig. 228*A*). Sporangiophores growing toward the integument are densely filled with cytoplasm and contain 10 to 20 nuclei. The nuclei often lie equidistant from one another and in a linear series. After growing through the opening in the integument, the distal end of a sporangiophore inflates to three or four times its original diameter and all of the proto-

[1] Thaxter, 1888 [2] Gussow, 1917. [3] Rees, 1932.
[4] Sawyer, 1929. [5] Speare, 1922.

plasm moves into the inflated portion (Fig. 228*C*). It is uncertain whether or not there is an increase in the number of nuclei during elongation of sporangiophores of *E. Muscae*. Certainly this is not the case in another species of *Empusa* where a four-nucleate hyphal body produces a conidiosporangium containing four nuclei.[1]

Development of a conidiosporangium of *E. Muscae* begins with a formation of a small mammilate outgrowth at the distal end of an inflated

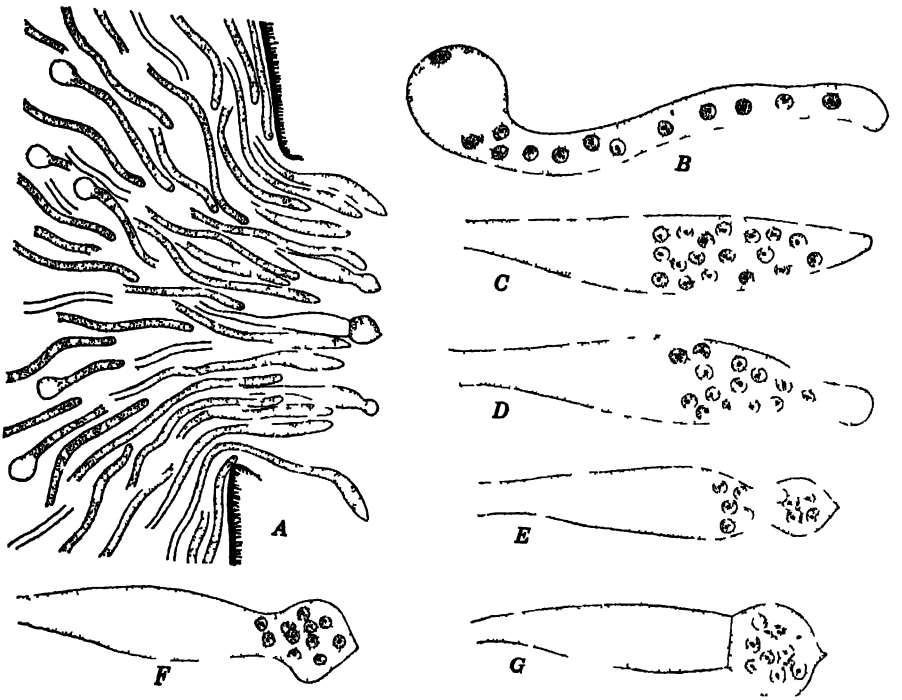


FIG 228.—*Empusa Muscae* Cohn. *A*, portion of the host with developing fructifications of the fungus. *B*, hyphal body elongating to form a sporangiophore. *C*, sporangiophore apex just before formation of conidiosporangium. *D–G*, successive stages in formation of a conidiosporangium. (*A*, × 160, *B G*, × 650.)

sporangiophore (Fig. 228*D–F*). The apex of the outgrowth swells, and most of the cytoplasm and all of the nuclei move into the swelling. There is then a formation of a cross wall that separates the globose outgrowth, the conidiosporangium, from the underlying sporangiophore (Fig. 228*G*). A lens-shaped, water-filled cavity next appears between the cytoplasm of the conidiosporangium and the transverse wall. Possibly, as in another closely related genus,[3] there is a secretion of a second transverse wall immediately next to the conidiosporangial protoplast. In any case, accumulation of water in the cavity eventually results in a hydrostatic pressure that bursts the lateral wall and suddenly squirts the

[1] Rees, 1932. [2] Olive, 1906; Goldstein, 1927. [3] Sawyer, 1931.

conidiosporangium outward for a few millimeters. This forcible discharge of a conidiosporangium does not involve any rupture of the sporangiophore apex.

If the discharged conidiosporangium comes in contact with a suitable host, it adheres to it and soon infects the host. If a conidiosporangium has fallen upon an unsuitable substratum, it sends out a short protuberance that becomes swollen at its apex and develops into a conidiosporangium similar to that from which it was derived. This may be indefinitely repeated until the secondary conidiosporangium lodges upon a suitable substratum or until the reserve food is exhausted.

E. Muscae may also form thick-walled resting spores within the body of a host. These have been considered parthenospores.[1] It is more

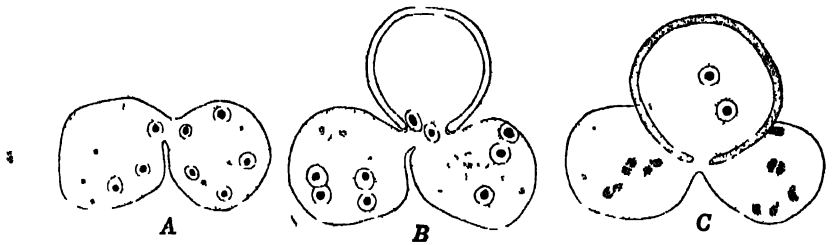


FIG. 229.—Sexual reproduction of *Empusa fumosa* (Speare) comb. nov. *A*, hyphal bodies at the beginning of conjugation. *B–C*, young and nearly mature zygotes. (*After Rees*, 1932.) (× 1900.)

probable that they are chlamydospores[2] since they are formed in old dead flies where the production of conidiosporangia is no longer possible. The chlamydospores are produced upon immature sporangiophores within the host and may be terminal or intercalary in position.

Sexual reproduction has not been observed in *E. Muscae*, but it has been found in two or three other species of *Empusa*. In *E. fumosa* (Speare) comb. nov. (*Entomophthora fumosa* Speare) sexual reproduction is by the conjugation of two adjoining hyphal bodies.[3] The four nuclei in each of the two hyphal bodies divide once.[4] The walls of the hyphal bodies break down in the region of mutual contact, and the two bodies become joined by a narrow isthmus (Fig. 229*A*). One nucleus from each protoplast comes to lie very close to the isthmus. There is then a development of a globular outgrowth from the isthmus, and, after it has attained approximately the size of a hyphal body, the two nuclei move into it. The binucleate protoplast of the outgrowth, now the zygote, then secretes a thick wall (Fig. 229*B–C*). Other species of *Empusa* form thick-walled parthenospores by outgrowth of a bud from a single hyphal body. These parthenospores are multinucleate.[5]

[1] Thaxter, 1888. [2] Goldstein, 1923. [3] Rees, 1932; Speare, 1922.
[4] Rees, 1932. [5] Riddle, 1906.

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CHAPTER XII

ASCOMYCETAE

Most of the Ascomycetae produce more than one type of spore, but all of them have a distinctive type of sporangium, the *ascus*, within which *ascospores* are produced. A very young ascus has a binucleate protoplast. Later on the two nuclei fuse, after which the fusion nucleus divides meiotically. Nuclear division generally continues until there are eight nuclei, but it may continue until there are 1,024 of them. After nuclear division ceases, the multinucleate protoplast gives rise to uninucleate ascospores by a unique type of endoplasmic cytokinesis.

Vegetative Structure. The plant body of some ascomycetes is a loosely interwoven mass of hyphae producing a mycelium similar to that found in a majority of the phycomycetes. More often, all or a portion of the mycelium is densely compacted into a pseudoparenchymatous structure of definite macroscopic form. The hyphae have what appear to be transverse walls. Actually, the so-called transverse wall is an incomplete septum with a central perforation. This incomplete septation is comparable to that found in certain of the siphonaceous green algae. The central perforation in a septum is frequently large enough to permit a streaming of cytoplasm from "cell" to "cell"[1] The portion of the protoplast between two successive septa generally contains one nucleus, but, as in *Dipodascus* and *Pyronema*, it may be multinucleate

Asexual Reproduction. A production of asci is contingent upon sexual reproduction or at least upon the development of sex organs. Spores other than ascospores are asexual reproductive bodies. Except for the numerous genera found in lichens, a large majority of the ascomycetes regularly produce one or more types of nonflagellate spores. In certain ascomycetes, as the powdery mildews (Erysiphaceae) and the blue molds (Aspergillaceae), reproduction is generally by means of asexual spores, since ascospores are only formed at the end of the growing season or under especial conditions. Asexual reproduction of the fungi just mentioned is by means of *conidia*. In *Erysiphe* the terminal portion of a free end of a single conidium may function as a *conidiophore* that cuts off a chain of conidia in acropetalous succession. Other genera, including *Aspergillus*, form many chains of conidia on a single conidiophore. If an ascomycete is one with the mycelium more or less densely compacted, the

[1] Buller, 1933.

conidiophores generally lie laterally abutting on one another in a continuous spore-forming layer. The layer is an *acervulus* when produced by a parasitic fungus and a *sporodochium* when produced by a saprophytic fungus. If the fertile layer lies in a cup- or flask-shaped cavity that is open from the beginning, the cavity and the surrounding tissue constitute a *pycnidium*, and the spores produced within it are *pycnospores*. In addition to forming conidia or pycnospores, a mycelium may also form large thick-walled spores. These *chlamydospores* are produced singly or in short catenate series. Instead of a formation of spores in acropetalous or basipetalous succession at the end of a hypha, there may be a simultaneous formation of them through the entire length of a hypha. Spores formed in this manner are often called *oidia*.

Sexual Reproduction. Sex organs of ascomycetes are developed singly at the apices of hyphae and are generally on short lateral branches. A mycelium may be homothallic or heterothallic. Irrespective of whether they are borne on the same mycelium or on different mycelia, the sex organs generally develop in such a manner that a male sex organ lies apposed to a female one. The protoplast within each of the paired sex organs may be uninucleate (*Eremascus*, *Erysiphe*) or multinucleate (*Pyronema*). In a few genera, as *Eremascus*, male and female sex organs are indistinguishable from each other. Generally, however, a male organ (*antheridium*) of an apposed pair is morphologically distinct from the female organ (*ascogonium*). An ascogonium may consist of a single cell or of more than one cell, and its distal end may be broadly rounded or may be prolonged into a definite *trichogyne* (Fig 248.1).

A union of protoplasts contained within the paired sex organs has been demonstrated for many species. If the two sex organs are alike, their apices become apposed, the walls disappear in the region of mutual juncture, and the two protoplasts fuse with each other. If the species has a distinct antheridium and ascogonium, the protoplast of the antheridium migrates into the ascogonium, either through a lateral pore or through the trichogyne. Union of the protoplasts may be followed by a union of the nuclei. This seems to have been clearly demonstrated for certain species with uninucleate sex organs.[1] The behavior of nuclei of multinucleate protoplasts has been a matter of dispute. In *Pyronema confluens* Tul. the fusion of nuclei in pairs has been affirmed[2] and denied.[3] The demonstration[4] that the number of nuclei in the ascogonium of this species increases at the time of fertilization and then decreases to approximately the original number seems to show that they fuse in pairs.

There are some ascomycetes that produce conidium-like bodies, known as *spermatia*, instead of producing antheridia. Ascogonia of these

[1] Harper, 1896, 1905. [2] Harper, 1900.
[3] Claussen, 1912. [4] Gwynne-Vaughan and Williamson, 1931.

species always have an elongate trichogyne which is frequently multicellular. The spermatia are often borne more or less remote from the ascogonium. They are generally borne superficially on the thallus and in a flask-shaped cavity (*spermogonium*) that looks very much like a pycnidium. Sometimes, however, the spermatia are not in spermogonia but are borne singly[1] or in clusters[2] within the thallus. If the species is one which has spermogonia, the trichogyne projects beyond the thallus. Spermatia that have become detached from a spermogonium may be transported to, and lodge against, the protuberant end of the trichogyne (Fig. 297*A*). If the spermatia are not in spermogonia, there is a growth of the trichogyne to a spermatium or a cluster of spermatia (Fig. 297*B*). The discovery[3] of empty spermatia united with a trichogyne indicates that the contents of a spermatium migrate into a trichogyne, but there has been no demonstration of migration of a male gamete nucleus down the trichogyne.

The protoplast (zygote) resulting from gametic union may develop directly into an ascus, or it may develop indirectly into one to many asci. However, a formation of asci may take place without any preceding gametic union. This is clearly evident when, as in *Eremascus*,[4] the protoplasts of two apposed sex organs do not unite, and each develops directly into an ascus (Fig 234). There may also be an indirect formation of asci from an ascogonium without a preceding gametic union. Such species may lack antheridia[5] or may have functionless antheridia.[6] Ascus formation in these species may be strictly parthenogenetic, or it may be preceded by a fusion in pairs of ascogonal nuclei.

Formation of Asci. All of the genera referred to the Protoascomycetae have a direct development of the zygote into a single ascus or a parthenogenetic development of a gametangium into an ascus. In the species with uninucleate gametangia,[4] there is a fusion of the two gamete nuclei in the young zygote, now the ascus. This ascus enlarges to several times its original size, and the zygote nucleus divides to form four or eight daughter nuclei during the course of this enlargement. Following this there is a formation of four or eight uninucleate ascospores (Fig. 233). Not all the cytoplasm of the ascus of a protoascomycete is included within the ascospores, and it is very probable that ascospores are formed by "free cell formation" just as in the Euascomycetae. In the one protoascomycete with multinucleate gametangia (*Dipodascus*),[7] only one nucleus from each gametangium functions as a gamete nucleus and the

[1] Dodge, B O., 1912. [2] Bachmann, 1912. [3] Bachmann, 1913.

[4] Stoppel, 1907; Guilliermond, 1909

[5] Cutting, 1909; Gwynne-Vaughan and Williamson, 1930; Ramlow, 1906; Fraser, 1913.

[6] Brown, 1915. [7] Dangeard, 1907; Juel, 1902.

single zygote nucleus divides to form many daughter nuclei. Thus, this species forms many ascospores within an ascus. The single ascus formed from the zygote of a protoascomycete is always without any enveloping sheath of sterile tissue

The indirect production of asci from the zygote is due to a formation of hyphal outgrowths (*ascogenous hyphae*). All genera with this type of ascus formation are referred to the Euascomycetae. In practically all of them there is an outgrowth of more than one ascogenous hypha from the zygote (Fig. 230) Almost all of the euascomycetes have an enveloping

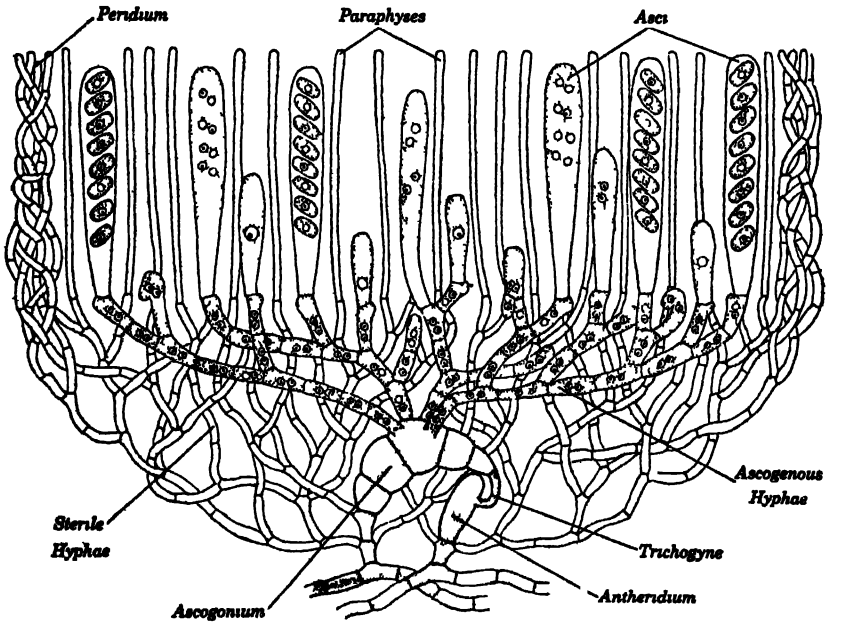


FIG. 230 —Vertical section of a hypothetical ascocarp showing relationship of sex organs, ascogenous hyphae asci, and sterile hyphae

tissue growing up around the ascogenous hyphae and the asci developed on them. The mass of asci and the enveloping tissue constitute the "fruiting body" or *ascocarp* An ascocarp usually contains only the asci derived from a single zygote, but there are cases, as *Pyronema*, where the asci derived from several zygotes are included in one ascocarp There are three general types of ascocarp: the *cleistocarp* (Fig 243*G*) that does not open at maturity; the open more or less cup-shaped *apothecium* (Fig. 298) in which the cavity is lined with a palisade-like layer of asci; and the flask-shaped *perithecium* (Fig. 256*D*), also lined with a palisade-like layer of asci but with an apical opening or pore.

An ascogonium may be unicellular, or it may be transversely septate, with the ascogenous hyphae growing out of one or more of the median

cells. In some cases the ascogenous hyphae are unbranched; more often they are profusely branched and with the branches intertwined with one another. Some species have ascogenous hyphae that do not become transversely septate until late in their development; but most of them have ascogenous hyphae that are transversely septate throughout all stages of development. In either case the cells at the distal end of the hyphae are binucleate. Among a majority of the species with closed ascocarps (cleistocarps), the asci are developed by gradual enlargement of a binucleate cell terminating a branch of an ascogenous hypha. Species in which the ascocarp is an apothecium or a perithecium generally have each branchlet of a fully developed, ascogenous, hyphal system terminating

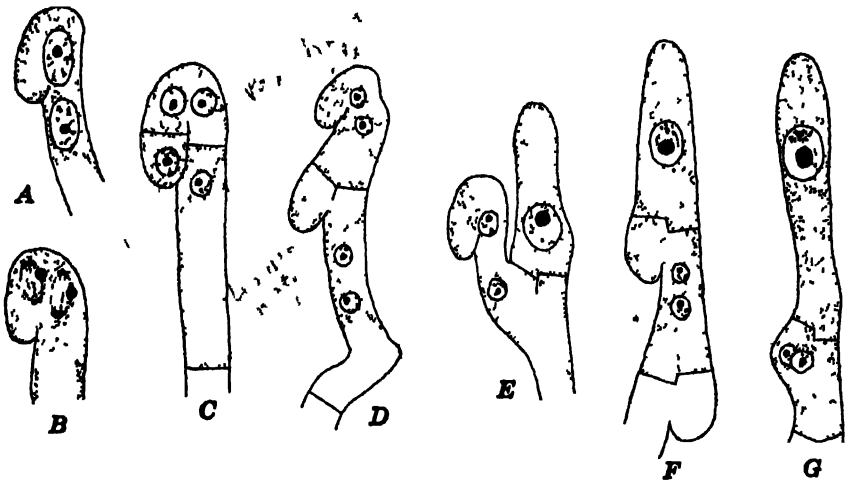


FIG 231.—Early stages in development of asci of *Pyronema confluens* (Pers.) Tul. *A–B* crozier-like bending of tip of ascogenous hyphae. *C D* young binucleate asci. *E–G*, asci after fusion of nuclei. (*After Claussen*, 1912.) (× 1,750.)

in a recurved, crozier-like, binucleate cell (Fig. 231). The two nuclei in this cell divide simultaneously. One pair of the resultant daughter nuclei lies in the arch of the crozier. One nucleus of the sister pair is at the extreme tip of the cell; the other lies in the upper region of the uncurved portion of the cell. Nuclear division is followed by a formation of transverse walls between the pairs of daughter nuclei. As a result the terminal cell of the branchlet is uninucleate, the penultimate cell is binucleate, and the antepenultimate cell is uninucleate (Fig. 231*C*). The binucleate penultimate cell is the one that develops into the ascus. The uninucleate terminal and antepenultimate cells may unite with each other to form a binucleate cell that subtends the young ascus.

A binucleate cell developing into an ascus enlarges to many times its original size and generally becomes club-shaped (Fig. 232). Early in the enlargement of an ascus there is a fusion of the two nuclei. During

further enlargement there is a division of the fusion nucleus, a division of its daughter nuclei, and a division of their daughter nuclei. Nuclear divisions generally stop at the octonucleate stage, but species are known in which it continues until there are 32,[1] 128,[2] 512,[3] or even 1,024[4] nuclei. The ascospores are formed after completion of the last series of nuclear divisions. At this time the nuclei are more or less pyriform and with a centrosome-like body at the pointed pole Soon each nucleus develops an umbrella-shaped set of radiating fibers that extend outward from the

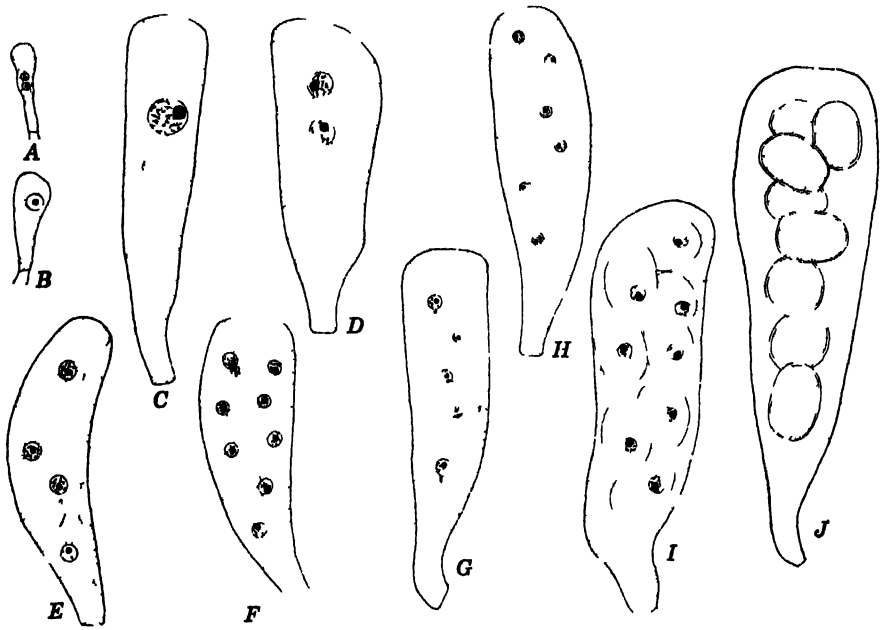


FIG 232 Stages in the development of asci of *Pythium aggregata* (Pk.) Farlow *A*, ascus before fusion of nuclei *B C* early and late uninucleate stages *D–F*, stages in development to octonucleate stage *G H* formation of ascospores *I–J*, formation of ascospore walls (× 650)

centrosome into the cytoplasm. Each curving set of rays grows downward until it is some distance beyond the rounded posterior pole of the nucleus; then it recurves to delimit a broad ellipsoidal mass of cytoplasm about the nucleus (Fig. 232*G-H*) The uninucleate protoplasts thus encircled by astral rays are the young ascospores. The portion of the cytoplasm of an ascus not included within the ascospores is the *epiplasm.* When an ascospore is first formed, its plasma membrane lies immediately next an inner delimiting membrane of the epiplasm (Fig. 232*I*). Later on there is a secretion of a spore wall about each naked spore and a gradual disappearance of the epiplasm as the spore walls

[1] Overton, 1906 [2] Sax, 1918 [3] Bessey, 1935.
[4] Dodge, B O , 1928 [5] Harper, 1897, 1905.

develop (Fig. 232*J*). The wall of a mature ascospore may be smooth or may have a characteristic ornamentation of spines or ridges. The number of ascospores produced within an ascus is not necessarily the same as the number of nuclei at the time of spore formation. Thus, a young octonucleate ascus may delimit ascospores around only two[1] or only four[2] of the nuclei and have the remaining six or four nuclei disintegrating as the epiplasm disintegrates. There are also cases[3] where two nuclei lie within a common set of astral rays delimiting an ascospore, and where there is regularly a formation of four binucleate spores in an octonucleate ascus. Conversely, an ascus that was octonucleate at the time of spore formation may contain more than eight spores when fully mature, because each of the eight spores has given rise to two daughter spores.[4] All species with an eight-spored ascus do not have the spores similarly arranged. Many species have the spores lying in a single linear series (Fig. 253), but other species have the spores in a double series (Fig. 232) or parallel to one another in a fasciculate cluster (Fig. 247*C*). A majority of ascomycetes have one-celled spores within a mature ascus, but species in which each spore becomes two-celled or more than two-celled before shredding are by no means unusual (Fig. 260*D*). A few species have the ascus wall disintegrating before the ascospores are shed;[5] but the great majority have the ascus wall remaining intact and rupturing at the distal end. The ruptured end may split irregularly, it may split into two parts, or there may be a lid-like opening of the ascus apex. Certain species have an explosive simultaneous discharge of many ascospores in a cloud-like mass and with a faintly audible puffing noise.[6] Spores ejected from an ascus may be hurled a distance of 35 cm.

Nuclear Cycle of the Ascomycetes. With the exception of certain yeasts, all the Protoascomycetae have a fusion of two gamete nuclei and a division of the zygote nucleus into four, eight, or more daughter nuclei. Although not actually demonstrated, there is a strong presumption that division of the zygote nucleus is a typical meiosis. If this is true, the zygote nucleus is the only diploid nucleus in the life cycle.

With one or two exceptions,[7] all the cytologically investigated species producing ascogenous hyphae have a fusion of two nuclei in the young ascus. In all cases the first division of the fusion nucleus is a reduction division. For many of the species with ascogenous hyphae the only doubling of the chromosome number is that in the ascus, and this is immediately followed by meiosis. Many mycologists think it highly probable that this nuclear cycle is found in all ascomycetes producing ascogenous hyphae. On the other hand, there seem to be certain well-established cases where gametic union results in ascogenous hyphae with

[1] Harper 1905. [2] Faull, 1912. [3] Dodge, B.O., 1927. [4] Lewis, 1911.
[5] Young, 1931. [6] Seaver, 1928. [7] Emmons, 1932

diploid nuclei and where nuclear fusion in the ascus produced a tetraploid nucleus. Here, a return to the original nuclear condition would involve a double reduction in the number of chromosomes, a phenomenon found nowhere else in the plant or animal kingdoms. Nuclei of the ascomycetes are so minute that cytological demonstration of a double reduction following a double fusion is an extremely difficult matter. In most of the cases where this is thought to have been shown,[1] it has been held that there is a halving of the number of chromosomes at the first division and another halving of the number in the third series of divisions. In other cases[2] there is a halving of the chromosome number in both the first and second divisions but no halving in the third series of divisions.

Studies on the genetic characters transmitted to each of the eight spores in asci of *Neurospora* shed some light on the problem of the nuclear cycle. All genetical studies[3] show that there is no segregation of characters in any pair of sister nuclei formed by the third series of divisions. Thus, there cannot be the supposed segregation of chromosomes at the third division. On the other hand, the genetical data have been interpreted both as showing that there is but one nuclear fusion antecedent to the formation of asci[4] and as showing that ascospore formation is preceded by two nuclear fusions.[5]

Origin and Evolution of the Ascomycetes. Two widely different hypotheses have been proposed to account for the origin of the Ascomycetae. According to one hypothesis they have arisen from the Rhodophyceae. Advocates of this hypothesis,[6] first proposed by Sachs,[7] point to the numerous similarities between reproductive structures of Ascomycetae and Rhodophyceae. These include the presence of a trichogyne on the female sex organ, the production of nonmotile male gametes (spermatia) that are transported to the trichogyne, and analogies between the ascogenous hyphae and the gonimoblast filaments of red algae. According to those who believe in the rhodophycean hypothesis, the most primitive of the Ascomycetae are those in which fertilization is effected by spermatia. They hold that ascomycetes with a direct production of asci from zygotes are reduced forms from ones with a more complicated mode of ascus formation.

According to another hypothesis, first proposed by DeBary,[8] the Ascomycetae have arisen from the Phycomycetae. Advocates of this

[1] Fraser, 1908; Fraser and Welsford, 1908; Fraser and Brooks, 1909; Carruthers, 1911; Gwynne-Vaughan and Williamson, 1932

[2] Gwynne-Vaughan and Williamson, 1931.

[3] Dodge, B.O., 1929, 1930, 1931, 1932; Lindegren, 1932, 1932*A*, 1933, 1934; Wilcox, 1928.

[4] Lindegren, 1932*A*, 1933, 1934. [5] Dodge, B. O., 1932.

[6] Dodge, B.O , 1914; Bessey, 1914, 1925; Thaxter, 1896; Harper, 1900; Bachmann, 1913.

[7] Sachs, 1875. [8] DeBary, 1887.

hypothesis[1] hold that the ascomycetes with a direct formation of asci from the zygote are the most primitive of all. It is also held that the evolution of ascogenous hyphae, the evolution of a trichogyne, and the evolution of fertilization by means of spermatia took place after the ascomycetan series had diverged from the ancestral stock. Adherents to the phycomycetan hypothesis interpret the presence of analogous structure in Ascomycetae and Rhodophyceae as a case of parallel evolution and not a derivation of one from the other.

Whatever the origin, evolution of the Ascomycetae was accompanied by the appearance of a unique type of endoplasmic cytokinesis (*free cell formation*) immediately following upon meiosis. It is equally possible for this to have appeared in a rhodophycean carposporangium with a diploid nucleus or in the zygote of a phycomycete. The question as to which of these two possibilities is the more probable hinges on the nature of the ascomycetes that have a direct development of a zygote into an ascus. Advocates of the rhodophycean hypothesis hold that all of these are reduced or degenerate forms. This is certainly true of the yeasts and their immediate allies. On the other hand, no valid reasons have been presented for thinking that *Eremascus*, *Dipodascus*, and related genera are reduced forms. Taken as a whole, the evidence seems to show that Ascomycetae with a direct formation of asci from zygotes are more primitive than others. This being the case, it is not a long jump from them to phycomycetes in which the protoplast of a germinating zygote divides into a number of spores. All that would be necessary to transform such a phycomycete into an ascomycete would be the establishment of the free-cell formation characteristic of ascomycetes.

Primitive Ascomycetae with a direct formation of spores from the zygote stand in much the same relationship to other ascomycetes as do the Bangioideae to the Florideae. In both the higher Ascomycetae and the higher Rhodophyceae (Florideae) there has been a shift to a condition where the germinating zygote sends out filaments (ascogenous hyphae or gonimoblasts) on which the sporangia are borne. In both cases this may be interpreted as a device that permits production of an unlimited number of spores following one gametic union. Among the ascomycetes, evolution to a condition where the zygote sends forth sporangial filaments has been accompanied by the introduction of an entirely new feature—the fusion of two diploid nuclei in a young sporangium. This quadrupling of the chromosome number is widespread among the genera producing ascogenous hyphae. On the other hand, there has been a dropping out of the fusion of gamete nuclei among many of the species producing ascogenous hyphae. This has resulted in a life cycle in which there is but one nuclear fusion—that which takes place in the ascus.

[1] Atkinson, 1915; Fitzpatrick, H. M., 1930; Gaumann, 1928; Guilliermond, 1928; Dangeard, 1907; Claussen, 1912.

Classification. For a long time the Ascomycetae were divided into three groups (subclasses or orders) based solely upon structure of the mature fruiting body. Genera forming apothecia were placed in the *Discomycetae*, those forming perithecia were placed in the *Pyrenomycetae*, and all other genera were placed in the *Plectomycetae*. The Discomycetae and Pyrenomycetae may be more or less natural groups; the Plectomycetae are certainly a heterogeneous assemblage. With the growth of knowledge concerning development of the fruiting body, there has been a realization that the feature of fundamental importance in classification of the ascomycetes is the mode of origin of the ascus. When classified according to this basis, they fall into the following two subclasses:

Protoascomycetae in which the ascus is formed directly from the zygote and in which the asci are borne singly on a mycelium and without any enveloping sheath of sterile tissue.

Euascomycetae in which there is an indirect formation of asci from a zygote. There is usually a formation of more than one ascus from a zygote, and the group of asci thus formed is usually surrounded by a common sheath of sterile tissue.

SUBCLASS 1. PROTOASCOMYCETAE

The Protoascomycetae comprise those genera in which the zygote develops directly into an ascus. Asci of Protoascomycetae are always borne singly on a mycelium and never in an ascocarp.

Only a few hundred of the known 25,000 species of Ascomycetae are referred to this subclass, and all of them are placed in a single order, the *Endomycetales*. Some of the Endomycetales are saprophytic; others are parasitic. A few of the saprophytic genera have a typical mycelium, but the great majority of them, including the yeasts, have a greatly reduced plant body and reproductive organs. Parasitic members of the order are almost exclusively restricted to animals and man, and many of them produce serious diseases of the host. The systematic position of certain parasitic genera assigned to the order is somewhat questionable since they have not been found producing typical asci. The order is divided into several families.[1]

Eremascus is one of the genera with a typical mycelium. One of the species (*E. fertilis* Stoppel) was first discovered growing as a mold on glasses of apple jelly.[2] This species has a branched, transversely septate mycelium. Cells in the older part of a mycelium are usually uninucleate; those toward tips of the hyphae contain from 2 to 15 nuclei. *E. fertilis* does not produce asexual spores.

Sexual reproduction may begin within five days after a mycelium has developed from an ascospore. Reproduction begins with an outgrowth

[1] Dodge, C. W., 1935. [2] Stoppel, 1907.

of small vertical protuberances. These are developed in pairs, one on each of two adjoining cells and near the transverse wall separating the two (Fig 233*A–C*). The tips of a pair of protuberances soon become apposed to each other, and the walls disappear in the region of mutual contact. Shortly afterward a nucleus migrates from each of the two cells into the fused protuberances, and the two nuclei soon unite with each other. Sooner or later there is the formation of a transverse wall (Fig. 233*E, G*) that cuts off the enlarging zygote, now the ascus, from the parent cells.[1] The zygote nucleus gives rise to eight daughter nuclei (Fig 233*H*), and it is very probable that, as has been shown for a closely related genus,[2] the

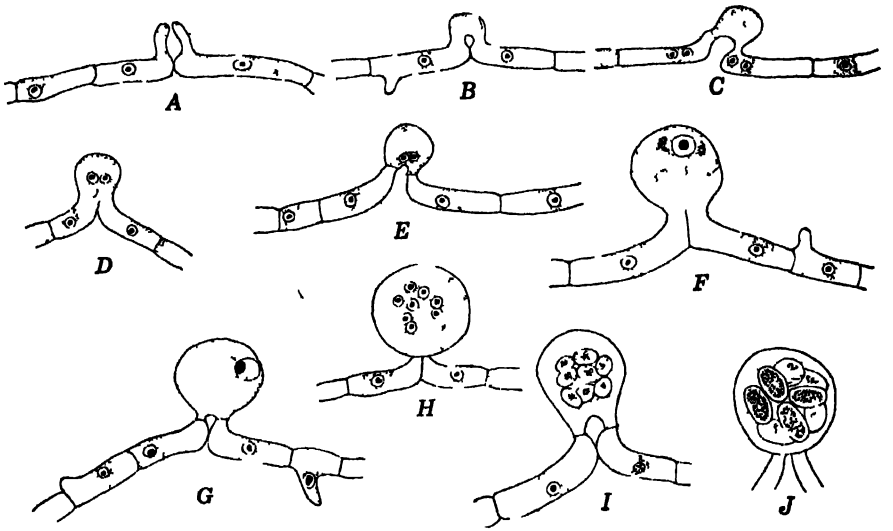


FIG 233.—*Eremascus fertilis* Stoppel *A-D, F* stages in conjugation *E*, young binucleate zygote *G* zygote after nuclear fusion *H* octonucleate zygote *I J*, formation of ascospores (*After Guilliermond* 1909)

first division is reductional The last step in ascus development is a free cell formation that divides the protoplast into eight uninucleate ascospores and a certain amount of epiplasm (Fig 233*I–J*). The ascospores are liberated by a disintegration of the ascus wall.

Instead of fusing with each other, both of an apposed pair of protuberances may develop into an ascus This is obviously due to parthenogenesis (Fig 234) So, also, is the development of an ascus from a solitary protuberance on a mycelium The same is also the case where a cell becomes greatly swollen, and its protoplast forms ascospores without sending out any protuberance

Dipodascus is another of the Protoascomycetae with a typical mycelium. There are two species The type species, *D. albidus* Lag., was first found growing saprophytically in slime fluxes exuding from

[1] Guilliermond, 1909; Stoppel, 1907 [2] Juel, 1902

trees. Its mycelium is sparingly branched and transversely septated into multinucleate cells of varying length (Fig. 235*A*). The other

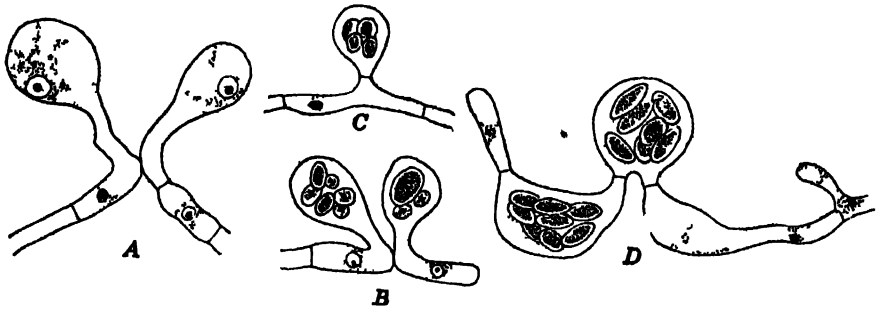


FIG. 234.—Parthenogenetic development of asci of *Eremascus fertilis* Stoppel (*After Guilliermond*, 1909)

species has uninucleate cells.[1] There is no regular formation of asexual spores, but under certain conditions a hypha may break up into a chain of oidia.[2]

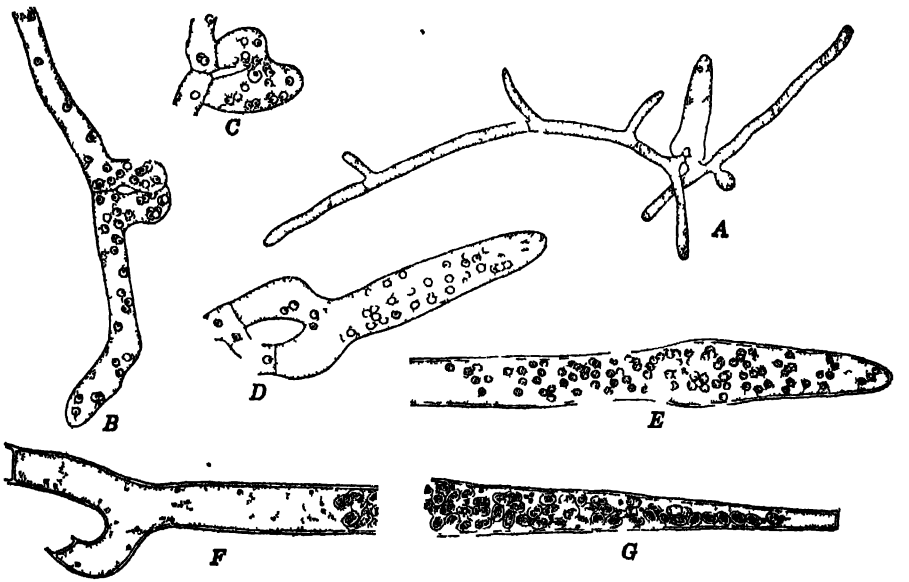


FIG. 235.—*Dipodascus albidus* Lag. *A*, thallus with a young ascus. *B–C*, early stages in conjugation. *D–E*, early and later stages in development of zygote. *F–G*, basal and upper portion of a zygote after the formation of ascospores. (*A*, *after Lagerheim*, 1892, *B–G*, *after Juel*, 1902) (*B–G*, × 675)

Sexual reproduction of *D. albidus* begins in much the same manner as in *Eremascus* and with a formation of two lateral protuberances adjacent to a transverse septum. Each of the two protuberances contains several nuclei.[3] There is soon a terminal fusion of the two protuberances

[1] Biggs, 1937 [2] Lagerheim, 1892 [3] Dangeard, 1907; Juel, 1902

(Fig. 235*B*). Following this, each protuberance forms a transverse basal septum which blocks off its protoplast from that of the parent cell. One gametangium (the male) of the fused pair develops no further, and most of its nuclei migrate into the other (the female) gametangium. The female gametangium continues growth until its height is 12 or more times that at the time of gametangial fusion. Shortly after the male nuclei migrate into the female gametangium, one of them fuses with a female nucleus. The fusion nucleus is somewhat larger than other nuclei in the young zygote (Fig. 235*C–D*). It divides and redivides to form 100 or more daughter nuclei, each of which becomes the nucleus of a young ascospore. The nonfusing gamete nuclei remain undivided[1] and persist until ascospore formation, when they lie in the epiplasm delimited about the ascospores (Fig. 235*F–G*). The apex of the ascus ruptures or gelatinizes at maturity, and the spores are extruded in a sticky matrix derived from the epiplasm. The extruded mass of spores often forms a sticky ball that remains attached to the ascus apex.[2]

The yeasts (*Saccharomycetaceae*) are Endomycetales in which there has been a complete or almost complete supression of mycelial development. However, when grown under certain conditions[3] many of the yeasts develop a distinctly mycelial type of plant body. The yeasts are generally considered reduced forms of genera closely related to *Eremascus*. They may be looked upon as unicellular mycelial forms in which there has been a permanent dissociation of the cells one from another.

Most of the yeasts are saprophytes that grow on substrata containing sugar. Such substrata include fruits, nectaries of flowers, and sugar-containing exudates from wounded plant tissues. A large majority of, but not all, the saprophytic yeasts break down sugars into carbon dioxide and alcohol when growing under anaerobic conditions. This is of vital importance to the baker and to the maker of alcoholic products. Certain species are much better than others in various industries involving fermentation, and cultures of these species are grown with the greatest of care to prevent contamination by less suitable species. Other yeasts are parasitic on animals, and most of them are distinctly pathogenic.

Yeasts are of two general types: those in which a cell divides into two daughter cells of equal size (*fission yeasts*); and those in which a cell buds off a small daughter cell (*budding yeasts*). There are also species in which cell division is intermediate between bipartition and budding.

Schizosaccharomyces is the best-known genus of fission yeasts. One of the species, *S. octosporous* Beyerinck, is found on fruits grown in regions with a mild climate. In this country it has been isolated from grapes grown in North Carolina and in California.[4] The cells in a

[1] Juel, 1902, 1921 [2] Lagerheim, 1892. [3] Guilliermond, 1920.
[4] Coker and Wilson, 1911.

recently inoculated and vigorously growing culture tend to be rectangular and some of them may be distinctly hypha-like; cells in older cultures tend to be shorter and more rounded. A cell of *S. octosporus* is uninucleate and with the cytoplasm containing several small vacuoles or one large vacuole. There is never any accumulation of glycogen.

Vegetative multiplication is by cell division. The nucleus of a cell divides into two daughter nuclei, and this is followed by a transverse cytokinesis that forms two daughter cells of approximately equal size (Fig. 236*A–B*). The daughter cells remain attached to each other for a time, but they eventually reflex and separate from each other.[1]

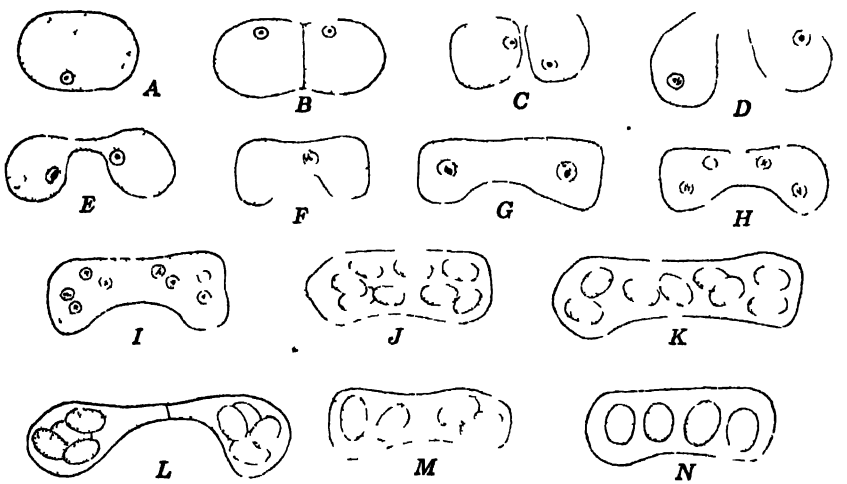


FIG 236.—*Schizosaccharomyces octosporus* Beyerinck *A*, vegetative cell *B*, cell division. *C F*, stages in conjugation *G I*, stages showing increase in number of nuclei before ascospore formation *J–K*, after formation of ascospores *L–N*, parthenogenetic formation of ascospores (× 1 950)

Sometimes each of the daughter cells divides again before separation takes place.

S. octosporus is homothallic[2] and sexual reproduction occurs in abundance two or three days after a culture has been inoculated on a solid medium. It begins with an end-to-end apposition of two rounded cells. Sometimes the two are sister cells; sometimes they are not. In either case, each of the two cells sends out a short protuberance and the two protuberances unite with each other to form a conjugation tube.[3] The two nuclei migrate into the conjugation tube and there fuse with each other (Fig. 236*C–E*). The conjugation tube broadens after this, and, according to the amount of broadening, the yoked cells develop into a dumbbell- or barrel-shaped zygote (the ascus). The zygote

[1] Coker and Wilson, 1911 [2] Guilliermond, 1931.
[3] Guilliermond, 1903, 1905; Coker and Wilson, 1911.

nucleus divides to form eight daughter nuclei (Fig. 236*F–I*), and this division is followed by a delimitation of eight uninucleate ascospores within the protoplast of the ascus (Fig. 236*J–K*). An ascus wall remains intact until germination of the ascospores within it. When an ascospore germinates, it enlarges somewhat and then divides transversely to form two daughter cells of equal size. Vegetative division continues for an indefinite number of cell generations. *S. octosporus* may also form ascospores without conjugation (Fig. 236*L–N*). These parthenogenetically developed asci usually contain four ascospores.

All of the budding yeasts have more or less ovoid cells. In *Saccharomyces cerevisiae* Hansen, one of the brewer's yeasts, there is a single conspicuous vacuole toward one pole of the cell. The cytoplasm con-

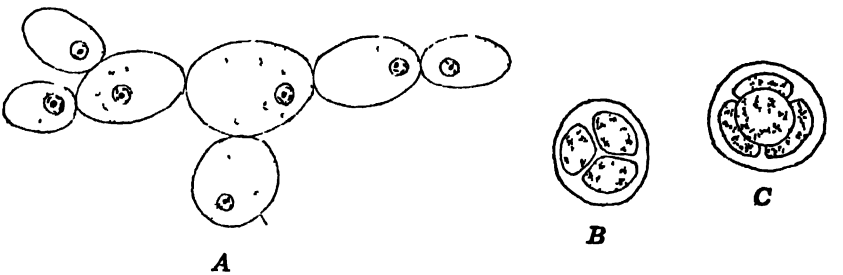


FIG. 237.—*Saccharomyces cerevisiae* Hansen. *A*, budding of vegetative cells. *B–C*, ascospores. (× 2,600.)

tains one small nucleus and numerous rounded or angular granules of reserve foods. The rounded granules are either glycogen or fats; the angular granules are protein compounds. Cell division of *S. cerevisiae* begins with a formation of a small outgrowth, the bud, at or near one pole of the cell. The nucleus divides as the bud is forming and one of the daughter nuclei migrates into the bud. A constriction of the plasma membrane in the plane of origin of the bud brings about a division into two daughter cells of very unequal size. The smaller of these, the former bud, enlarges rapidly, but it often produces a new bud before its enlargement is completed (Fig. 237*A*). Usually there is not an immediate separation of a bud from its larger sister cell. Because of this, the cells of *S. cerevisiae* tend to lie in short branched or unbranched chains.

Many of the budding yeasts also reproduce sexually. In one of them (*Zygosaccharomyces Barkeri* Saccardo and Sydow) conjugation takes place (Fig. 238) in much the same manner as in *Schizosaccharomyces octosporus*.[1] There is a fusion of two gamete nuclei in *Z. Barkeri*, but the zygote nucleus divides to form only four daughter nuclei. Parthenogenesis has not been demonstrated in *Z. Barkeri*, but it has been shown[2] to be of rather widespread occurrence in certain other conjugating species

[1] Barker, 1901 [2] Guilliermond, 1920.

of *Zygosaccharomyces*. Until very recently it has been assumed that most species of *Saccharomyces* are wholly parthenogenetic. Within the past three years four species of this yeast have been shown[1] to have the ascospores conjugating in pairs at the time of germination.

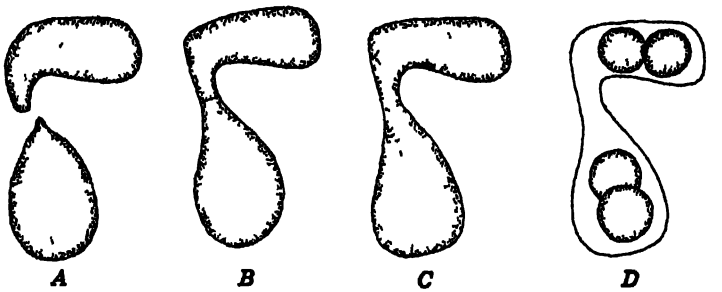


FIG 238.—*Zygosaccharomyces Barkeri* Saccardo and Sydow. *A–C*, stages in conjugation. *D* ascospores. (*After Barker*, 1901.) (× 1,500.)

There is considerable justification for an assumption that nuclear fusion in zygotes of *Schizosaccharomyces* and *Zygosaccharomyces* is followed by meiosis and that the vegetative cells have a haploid number of chromosomes. However, this generalization cannot be extended to all conjugating yeasts. In *Saccharomycodes Ludwigii* Hansen[2] and the

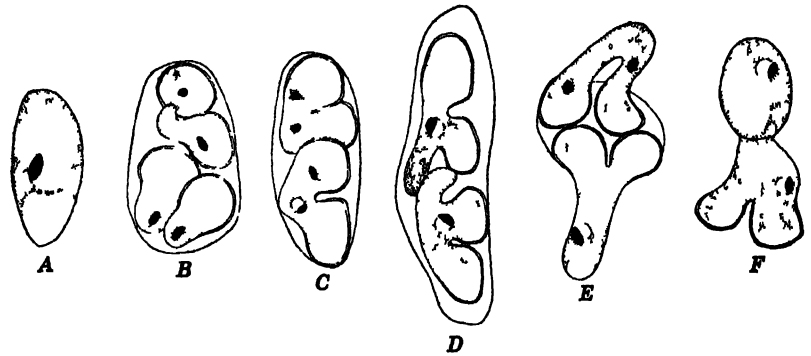


FIG 239.—*Saccharomycodes Ludwigii* Hansen. *A* vegetative cell. *B*, germinating ascospores. *C–E*, stages in conjugation of germinating ascospores. *F*, the first cell division after conjugation. (*After Guilliermond*, 1905.)

species of *Saccharomyces* just mentioned, conjugation takes place when the ascospores germinate and not just before they are formed (Fig. 239). The cell resulting from fusion of two germinating ascospores may undergo repeated vegetative division before there is a formation of a new suite of ascospores. It is very probable that the vegetative cells of these yeasts are diploid and that meiosis is delayed until just before ascospore formation.

[1] Winge, 1935. [2] Guilliermond, 1903, 1905.

SUBCLASS 2. EUASCOMYCETAE

The Euascomycetae include all the Ascomycetae in which the asci are formed on ascogenous hyphae arising from a zygote or from a parthenogenetically developing ascogonium. Practically all of the Euascomycetae produce ascocarps containing many asci. The subclass includes all but about 500 of the known 25,000 species of ascomycetes.

There are no known transitional forms leading from the Protoascomycetae without ascogenous hyphae to the Euascomycetae with well-developed ascogenous hyphae. Most mycologists think that the Aspergillales are the most primitive of the subclass. Primitive characters found among the Aspergillales include: an ascocarp in which the sterile jacket layer (*peridium*) is not open at maturity; asci developing directly from terminal cells of the ascogenous hyphae; and an irregular arrangement of the asci within an ascocarp. The derivation of the more advanced Euascomycetae from the Aspergillales is uncertain. The Aspergillales may have given rise to the discomycetes and these to the pyrenomycetes, or vice versa. There is also the possibility that the discomycetes and the pyrenomycetes represent two divergent evolutionary lines from the lower Euascomycetae.

During the past 40 years there has been a growing tendency to abandon the classification of ascocarpic ascomycetes into Plectomycetae, Discomycetae, and Pyrenomycetae. Instead, mycologists[1] have separated the Euascomycetae into a number of orders, but they are in marked disagreement as to the number that should be recognized. Of the orders described in this chapter the Pezizales, Helvellales, Phacidiales, and Hysteriales are usually considered Discomycetae; and the Hypocreales, Sphaeriales, and Dothidiales are considered Pyrenomycetae. The Euascomycetae may be divided into the following 12 orders:

ORDER 1. ASPERGILLALES

The Aspergillales, also known as the *Plectascales*, have a closed ascocarp (cleistocarp) in which the outer sterile portion (peridium) is composed of loosely or compactly interwoven hyphae. The asci lie irregularly distributed within the ascocarp. The order contains more than 30 genera and 800 species.

Penicillium is a saprophytic genus that grows on decaying vegetables, fruits, meats, and a great variety of moist plant and animal substances. Most species cause economic loss, but a few of them, especially those involved in ripening of Camembert and Roquefort cheeses, are of economic benefit. There are also a few species pathogenic to man and

[1] Clements and Shear, 1931; Gwynne-Vaughan and Barnes, 1927; Schröter, Lindau and Fischer, 1894–1897; Gaumann, 1928; Bessey, 1935.

other animals. Four hundred forty-three species are recognized in a recent monograph of the genus.[1] The mycelium of *Penicillium* may grow superficially upon or penetrate deeply into the substratum. It is composed of freely branched hyphae with thin-walled cells, each generally with more than one nucleus. In some species the mycelium may become compacted into a sclerotium.

Asexual reproduction is by the formation of brush-like tufts of "conidia" at the tips of conidiophores. A conidiophore grows vertically from the mycelium and to a more or less definite height. It may consist of a single axis terminating in a penicillate tuft, or it may be branched, with each branch terminating in a tuft (Fig. 240). A conidiophore, or each branch of it, terminates in several uninucleate conidiiferous cells or *sterigmata*. A sterigma of *Penicillium* is not homologous with the sterigma found in basidiomycetes. Spore formation begins with a division of the nucleus and a migration of one daughter nucleus into the narrow apex of a sterigma. The terminal portion of the sterigma is then cut off as a short cylindrical cell, and the protoplast secretes a spore wall that lies free from the original enclosing wall; in other species it secretes a spore wall that is fused with the original wall.[2] Thus the conidia of *Penicillium* are really aplanospores or akinetes. Additional cells are cut off in acropetalous succession at the sterigma apex, and the protoplast of each develops into a spore. Accordingly as the spore wall is free from or united with the original cell wall, the spores in a chain lie a short distance from, or abut upon, one another.

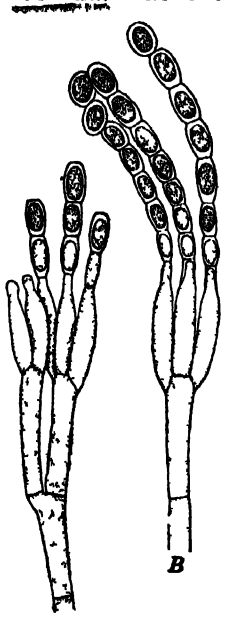


FIG. 240.—Conidia of *Penicillium* sp. (× 975.)

Most of the species known to produce asci belong to a single section of the genus.[1] Certain of these species are heterothallic and only form asci when there is an intermingling of two mycelia.[3] The structure of the sex organs and the development of asci vary from species to species.[4] *P. vermiculatum* Dang. is one of the species with a simple type of ascogonium. It has a mycelium of uninucleate cells, and its ascogonia are developed from erect unicellular branches.[5] A young ascogonium is uninucleate, but, as it elongates, the nucleus divides and redivides to form 32 or 64 daughter nuclei (Fig. 241*A–B*). A slender uninucleate antheridial branch grows up in a lax spiral that makes several turns about the developing ascogonium. The antheridial branch eventually forms a short, some-

[1] Thom, 1930 [2] Thom, 1914, 1930. [3] Derx, 1925.
[4] Dodge, B. O., 1933; Emmons, 1935. [5] Dangeard, 1907.

what inflated, uninucleate antheridial cell at its distal end. The tip of the antheridial cell is apposed to the ascogonium, and there is a dissolution of cell walls in the region of mutual contact (Fig 241*C–D*). It has been held[1] that there is no gametic union after the establishment of connection between antheridial and ascogonial protoplasts. However, the demonstration[2] that *P. vermiculatum* is heterothallic implies that there is a gametic union. Entangled sterile hyphae now grow up about the united

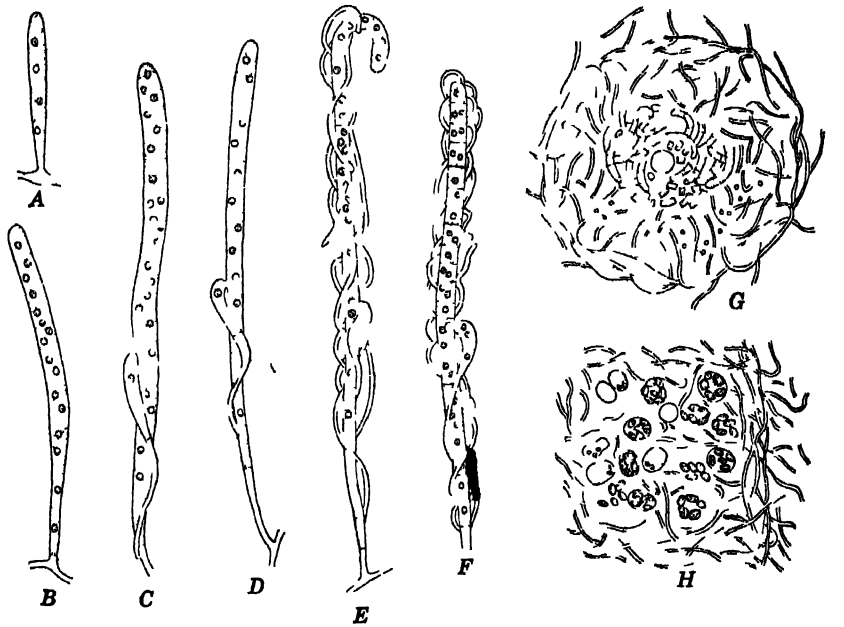


FIG. 241 *Penicillium vermiculatum* Dang. *A B* young ascogonia *C–D* ascogonium after development of the antheridium *E* ascogonium beginning to be surrounded by sterile hyphae *F* after the transverse septation of the ascogonium *G* transverse section of a young ascocarp showing the ascogonium surrounded by ascogenous hyphae (shaded) and sterile hyphae *H* portion of nearly mature ascocarp showing the asci intermingled with sterile hyphae (*After Dangeard*, 1907) (× 450)

antheridium and ascogonium (Fig 241*E–G*) and develop into the loosely felted outer region of the mature ascocarp. Meanwhile, the ascogonium becomes transversely divided into a row of binucleate cells (Fig 241*F*), each of which sends out one or more branched ascogenous hyphae, also composed of binucleate cells. The details of ascus development are unknown for *P. vermiculatum*. The mature asci lie irregularly distributed throughout the loose meshwork of hyphae comprising the central region of an ascocarp (Fig 241*H*). They are subglobose and generally with four to [illegible] ellipsoidal ascospores.

[1] Dangeard, 1907 [2] Deix, 1925

ORDER 2. ERYSIPHALES

The Erysiphales (sometimes called the Perisporales) are parasites that grow superficially on the host. The ascocarp is a more or less globose cleistocarp with a compact pseudoparenchymatous jacket layer (peridium) that has no opening. Most members of the order have a layer of parallel asci at the base of the cavity within the peridium, but a few of them have the layer reduced to a single large ascus.

The powdery mildews (Erysiphaceae) are the only family of the order in which the life history has been studied in detail. *Erysiphe*, the type genus, grows on a wide variety of hosts, including many cultivated plants, and over 50 species have been described. Its mycelium is composed of short uninucleate cells. The mycelium grows superficially on the host, either upon stem or leaf. Food is obtained by means of modified, one-celled, haustorial branches that pierce the walls of the epidermal cells of the hosts. Haustorial branches of most species develop into globular or pyriform swellings within the protoplast of the host cell (Fig. 242*A*), but in one species the haustoria have several parallel tubular processes.[1]

Asexual reproduction takes place shortly after the mycelium has become established upon a host and begins with an upgrowth of numerous short, erect, unicellular branches (conidiophores) from the mycelium. A unicellular conidiophore may cut off conidia in acropetalous succession from its distal end (Fig. 242*B–I*), or it may divide into a long stalk cell and a short terminal cell that successively cuts off conidia. Conidia are formed in profusion throughout most of the growing season. There is an immediate germination of detached conidia that have fallen upon a suitable host, and within a few days the new mycelium begins to form conidia.

Sexual reproduction of *Erysiphe* does not begin until the growing season of the host is drawing toward a close. Sex organs are developed at the ends of hyphae which have grown together in pairs and are twisted about each other. The terminal cell of one hypha develops directly into the somewhat broadened uninucleate ascogonium (Fig. 243*A*). The terminal cell of the other hypha divides transversely into two daughter cells of unequal length. The distal cell is the antheridium; the other is the stalk cell.[2] The antheridial and ascogonial walls disappear at the region of mutual contact to form a pore through which the protoplast of the antheridium migrates into the ascogonium.[3] Fusion of the gamete nuclei is followed by an immediate division of the zygote nucleus into five to eight daughter nuclei (Fig. 243*B*). The multinucleate ascogonium next

[1] Smith, G., 1900. [2] Harper, 1896.

[3] Certain mycologists, including Dangeard (1907), Winge (1911), and Eftimiu (1929), hold that there is no migration of the antheridial protoplast into the ascogonium in the Erysiphales.

becomes a row of four to five cells by a formation of transverse septa.[1] In this row the penultimate cell has two or more nuclei (Fig. 243*C*). Several stout processes grow out from the upper side of the penultimate cell and each of them develops into an ascogenous hypha two or three cells in length (Fig 243*D*). The ascogenous hyphae are so densely intertwined that their development cannot be followed in detail, but it has been shown[1] that those cells which develop into asci are binucleate and inter-

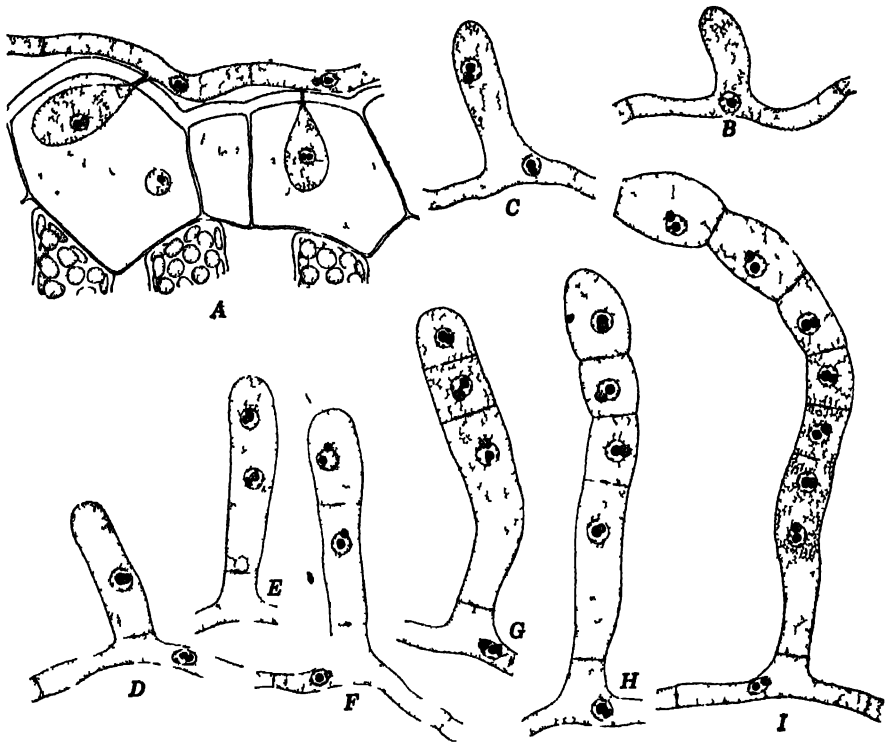


FIG 242 —*Erysiphe cichoraceum* DC *A* portion of a vegetative hypha with haustoria in epidermal cells of host *B I*, successive stages in development of conidia (× 650)

calary in position Cells of the ascogonous hyphae destined to become asci soon increase greatly in size (Fig 243*E–F*); the remaining cells of the ascogenous hyphae lose their protoplasts and become compressed as the asci develop.

The sex organs become surrounded by a layer of densely compacted sterile hyphae immediately after fertilization (Fig. 243*A–C*). These hyphae arise chiefly from the cell subtending the ascogonium. At first the ensheathing layer (peridium) is one cell in thickness, but, by the time the ascogenous hyphae appear, it has become three or more cells in thickness Eventually it becomes a layer, 6 to 10 cells in thickness, in which

[1] Harper, 1896

cells in the outer half are thick-walled and without protoplasts (Fig. 243*F–G*). Certain superficial cells in the outermost sterile layer develop into elongate appendages which may or may not be branched toward their apices.

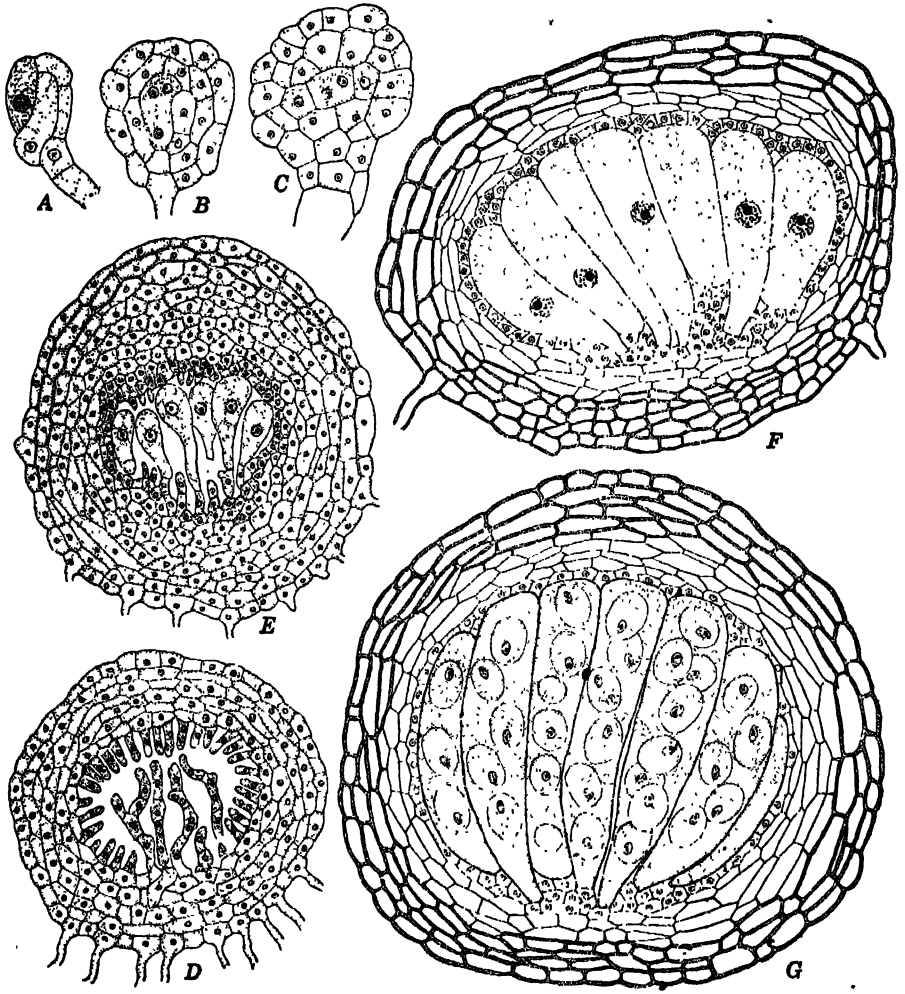


FIG. 243.—*Erysiphe aggregata* (Pk.) Farlow. *A*, ascogonium encircled by sterile hyphae. *B*, multinucleate ascogonium. *C*, after transverse septation of ascogonium. *D*, young ascocarp containing ascogenous hyphae. *E–G*, successive stages in development of ascocarp and asci. (*A–C*, × 975; *D*, × 650; *E–G*, × 480.)

As this peridium is developing, there is a union of the two nuclei in each young ascus (Fig. 232). Following this, each ascus enlarges greatly, and during enlargement the fusion nucleus divides and redivides to form eight daughter nuclei. Division of the fusion nucleus is meiotic, and there is considerable evidence (page 421) for thinking that this involves a

double reduction in the chromosome number. Asci of some species of *Erysiphe* form eight ascospores after the octonucleate stage of ascogonial development (Fig. 243*G*). Asci of other species have a free cell formation around only two of the eight nuclei in an octonucleate ascus; the remaining six nuclei lie in the epiplasm surrounding the two ascospores. Ascospores of many species of *Erysiphe* are not fully ripened and capable of germination until the following spring.

A mature ascocarp usually remains attached to the host, but it may become accidentally detached and blown about by the wind. The peridium usually remains intact over winter, and there is no liberation of ascospores until the following spring. Opening of the ascocarp may, as in *E. graminis* DC.,[1] be due to a transverse splitting in the equatorial plane, followed by a shedding of the upper half of the peridium. In *E. graminis* there is a forcible ejection of ascospores from the exposed asci and an ejection with sufficient force to hurl them more than 20 mm. Ascospores falling upon a suitable host germinate immediately, and within a few days there is a production of conidia by the mycelium developing from an ascospore. The conidia, in turn, give rise to new mycelia producing conidia. When conditions are favorable, this may result in a rapid spreading of the fungus to a large number of individuals of the host species.

ORDER 3. HYSTERIALES

The Hysteriales have small elongate ascocarps which develop a longitudinal slit-like opening as they become mature. The asci lie in a palisade-like layer at the base of an ascocarp. The order includes some 25 genera and 280 species.

Ascocarps of the Hysteriales are often interpreted as apothecia that show an approach toward a perithecial type. There are equally good grounds for considering them cleistocarps with a longitudinal dehiscence at maturity.

Lophodermium is a parasitic genus with approximately 30 species. Certain of them, including *L. pinastri* (Schrad.) Chev., are parasitic upon leaves of conifers and cause a serious defoliation when seedlings of the host are infected. Other species are parasitic upon angiosperms. Some of these latter species are restricted to a single host; others, including *L. hysterioides* (Pers.) Sacc., infect a rather wide range of hosts.

Germinating ascospores of both *L. pinastri* and *L. hysterioides* produce a hypha that grows through a stoma and then develops into a mycelium that invades the underlying mesophyll. Eventually there is a development of a compact subcuticular or subepidermal sclerotial mass (Fig. 245*A*). Surface cells of the sclerotium develop into a palisade-like layer

[1] Salmon, 1903.

in which each cell cuts off a succession of acicular spore-like bodies (Fig. 244*C*). These bodies are generally considered conidial in nature, and the whole reproductive area is called a pycnidium. If they are asexual, the reproductive area should be considered an acervulus rather than a pycnidium. Recently[1] these "acervuli" have been interpreted as spermogonia in which each spermatiophore cuts off a succession of acicular spermatia The best argument in favor of their spermatial nature is the failure of all attempts[2] to germinate the conidia.

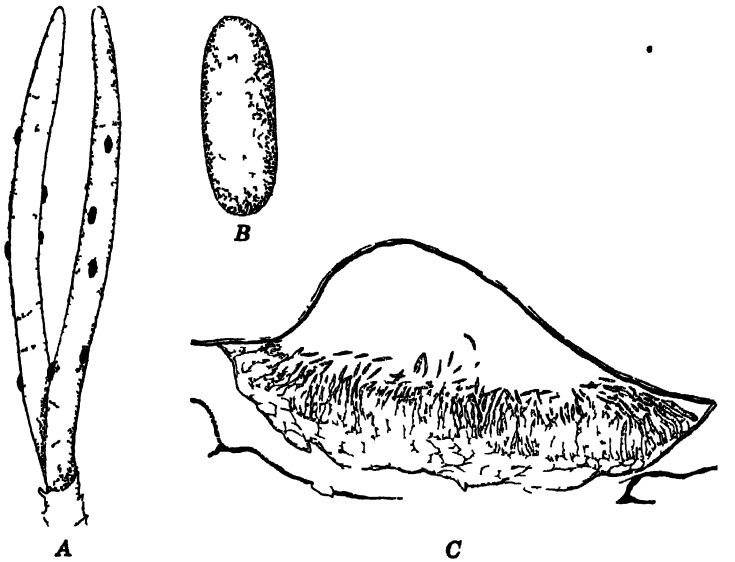


FIG. 244.—*Lophoderium pinastri* (Schrad.) Chev. *A*, pine needles with mature ascocarps *B*, surface view of an ascocarp *C*, vertical section of an "acervulus." (*A–B, after Jones*, 1935, *somewhat modified C from Likhité* 1926.)

L. pinastri seems to be heterothallic and only to have a development of ascocarps (Fig 244*A–B*) when there is a multiple infection of the host.[3] The production of ascogonia, the first step in the production of an ascocarp, takes place late in summer, while the leaves are still attached to the host. Later stages in ascocarpic development are completed during the winter and after abscission of the leaves Ascogonia of *L. pinastri* are flask-shaped and with the upper portion prolonged into a trichogyne.[1] Some of the ascogonia develop intermingled with the spermatiophores; others develop independent of the spermogonia (Fig. 245*B–C*). In the first case the ascogonia seem to be fertilized by spermatia developed within the same spermogonium; in the second they seem to be fertilized by spermatia exuding from spermogonia.

Differentiation of ascogonia is followed by a rapid enlargement of the sterile tissue into what eventually becomes the peridium of the mature

[1] Jones, 1935 [2] Likhité, 1926; Jones, 1935 [3] Langner, 1933

ascocarp Accordingly as an ascocarp is developed within a spermogonium or independent from it, the ascocarp is overarched by both the epidermis and cuticle of the host or by the cuticle only The subepidermal or subcuticular portion of a young peridium soon becomes a dark-colored tissue, the *epithecium,* the portion beneath this, the *hypothecium,* remains light colored The epithecium and hypothecium soon

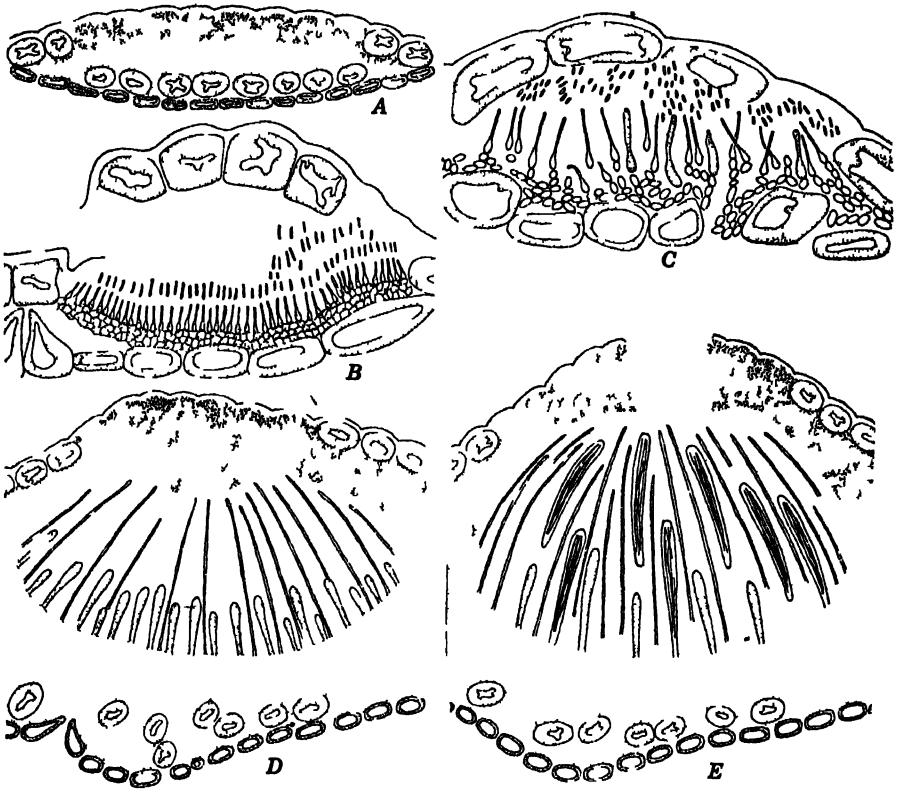


FIG 245 —*Lophodermium pinastri* (Schrad) Chev *A* very young ascocarp *B,* spermogonium *C* spermogonium containing ascogonia (shaded) *D–E* ascocarps with young and mature asci (*After Jones* 1935 *somewhat modified*) (4 *D E* × 265, *B,* × 600 *C,* × 550)

separate from each other along the plane of mutual contact, and erect hyphae (paraphyses) grow into the ascocarpic cavity thus developed Ascogenous hyphae ramifying through the hypothecium now grow up to the floor of the ascocarpic cavity and there produce asci Cells of ascogenous hyphae developing into asci may have (*L pinastri*)[1] or may lack (*L hysterioides*)[2] typical croziers In either case a mature ascus contains eight acicular ascospores.

[1] Jones, 1935 [2] Likhité, 1926

Coincident with appearance of the first asci, there is a differentiation of a tubular internal chamber along the saggital axis of the epithecium (Fig. 245*D*). This chamber becomes loosely filled with hyphae whose inflated terminal cells have living protoplasts. When the asci are mature, these somewhat mucilaginous hyphae absorb water in quantity, and the resultant hydrostatic pressure causes a longitudinal splitting of the epithecium (Fig. 245*E*). The exposed asci then eject their ascospores through the fissure in the epithecium.

ORDER 4. PHACIDIALES

The Phacidiales have a flattened rounded ascocarp in which the overarching peridium opens at maturity by rupturing into stellate fissures or by developing a circular pore. The order includes approximately 775 species—some parasitic, some saprophytic.

Rhytisma, a genus with about 25 species, causes conspicuous black areas on leaves of various hosts. Because of its color, the fungus is often known as *tar spot*. *R. Acerinum* (Pers.) Fries, parasitic on various species of maple, is the best-known species (Fig. 246). Ascospores of this species are discharged in the spring, and, when they fall upon a leaf of the host, they soon germinate to form a mycelium of short uninucleate cells. The mycelium is intracellular, and it invades all tissues of an infected area, including the upper and lower epidermis. At first growth is most active in the upper epidermis, and each of these cells becomes filled with densely compacted hyphae.[1] Eventually the mesophyll and lower epidermis also become filled with densely compacted hyphae. The hyphae adjoining outer walls of cells in the upper epidermis next secrete a dark-colored substance that fills all interhyphal interstices; the remaining hyphae within the upper epidermis continue growth. Growth of hyphae in the epidermis is accompanied by a rupturing or partial disintegration of anticlinal walls in the epidermal cells, and this is followed by a growth of the hyphal mass to several times the original thickness of the epidermis.

Asexual reproduction is by the formation of conidia. The conidiiferous area is circular in outline and is differentiated from the mycelium within what was formerly the epidermis. The outer dark-colored portion of the intra-epidermal mycelium forms a protective covering over the conidiiferous area, and the conidia are developed immediately below it. A superficial cell of the conidiiferous tissue divides into a short basal cell and a long cell, the conidiophore,[1] which cuts off acicular conidia in acropetalous succession at its upper capitate end. The continued production of conidia eventually causes a bulging and an eventual rupture of the black overroofing fungus tissue. A viscous

[1] Jones, 1925.

liquid containing innumerable conidia then exudes through the opening. The conidium-forming area is usually called a pycnidium, but it would be more appropriate to call it an acervulus[1] because the enclosing sterile tissue is not open from the beginning. The conidia have been considered nonfunctional[2] since they could neither be induced to germinate nor to produce an infection when inoculated on leaves.

Ascocarp development begins in the autumn and generally upon leaves shed from the host. An acervulus that has discharged most of its conidia may develop into an ascocarp, but most ascocarps are formed *de novo* and toward the margin of the blackened infected area. At this time the mycelium consists of an outer black zone of densely compacted hyphae, a median colorless zone of loosely interwoven hyphae, and an inner, somewhat darkened zone of compacted hyphae. Ascocarp develop-

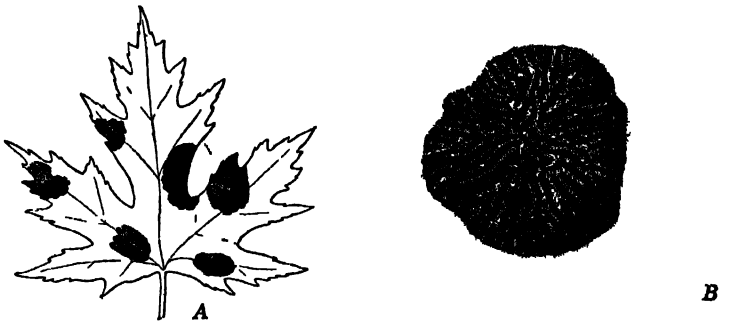


FIG. 246.—*Rhytisma Acerinum* (Pers.) Fries. *A*, leaf of maple with ascocarps. *B*, ascocarp. (*A*, × ½, *B*, × 3.)

ment commences with an enlargement of a disk-shaped area in the middle zone, the cavity thus formed containing many loosely interwoven branched hyphae. Several ascogonia are developed low on the hyphal system filling the cavity. There is never a development of antheridia. Each ascogonium is a lateral hyphal branch two to five cells long. The lowest cell is a stalk cell, the next cell above that is the ascogonium proper, and the cell or cells above the ascogonium proper constitute the trichogyne.[2] The stalk and trichogyne cells are usually uninucleate, and the ascogonial cell is always multinucleate. Sooner or later there is a disappearance of all transverse walls in the branch except that between stalk and ascogonium. All the nuclei and cytoplasm of the trichogyne migrate into the ascogonium, which soon sends out multinucleate outgrowths—the ascogenous hyphae. Nuclei in both the ascogonium and the ascogenous hyphae tend to lie in pairs, but there is no fusion of the paired nuclei. Eventually the ascogenous hyphae

[1] Gaumann and Dodge, 1928. [2] Jones, 1925.

develop transverse septae that divide them into binucleate cells and develop asci directly from terminal cells without forming the usual croziers. Unlike most other ascomycetes, fusion of the two nuclei in the ascogenous cell is delayed until the ascus has become elongate and club-shaped. The fusion nucleus divides into eight daughter nuclei, and an ascospore is cut out about each daughter nucleus. The ascospores elongate to many times their original length and come to lie parallel

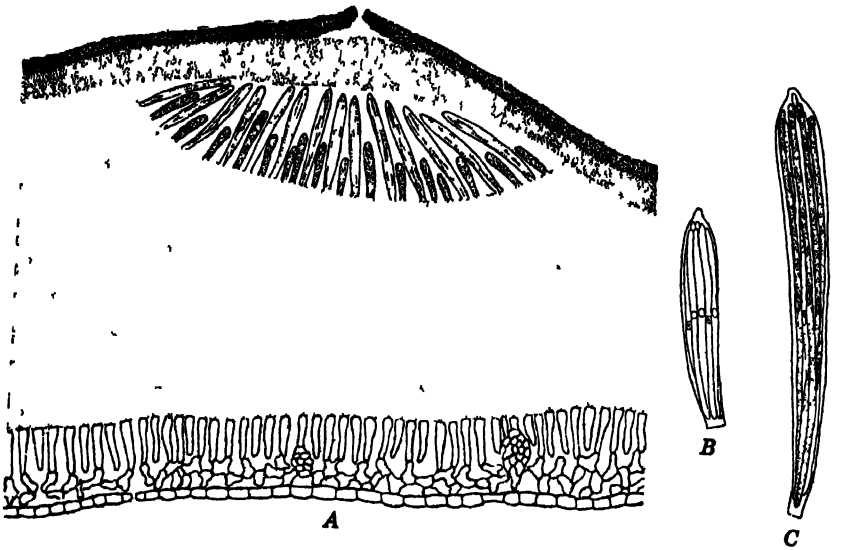


FIG. 247 - *Rhytisma Acerinum* (Pers.) Fries. *A*, vertical section of a mature ascocarp. *B*, *C*, young and mature asci. (*A*, × 185, *B*, *C*, × 650.)

to one another in a fasciculate cluster in which one spore is encircled by the other seven (Fig. 247*B-C*).

As the asci are maturing, there is a disintegration of an internal strip of cells in the lower portion of the compact roof of the ascocarp (Fig. 247*A*). The slot-like cavity thus formed becomes filled with a mucilaginous substance that imbibes water. With continued imbibition there is eventually a development of a hydrostatic pressure sufficient to burst the overlying portion of the roof. Rupture of the tissue underlying the cavity is due to a swelling of the paraphyses and asci. When the asci are exposed, there is a forcible ejection of ascospores in a small dust-like cloud that shoots upward for a millimeter or more.[1] A few minutes after puffing, there is an ejection of another puff of ascospores, and intermittent puffing continues until all the ascospores have been discharged.

[1] Jones, 1925.

ORDER 5. PEZIZALES

The Pezizales, familiarly known as the cup fungi, have a more or less cup-shaped apothecium lined with a layer of parallel asci. The order includes some 4,700 species.

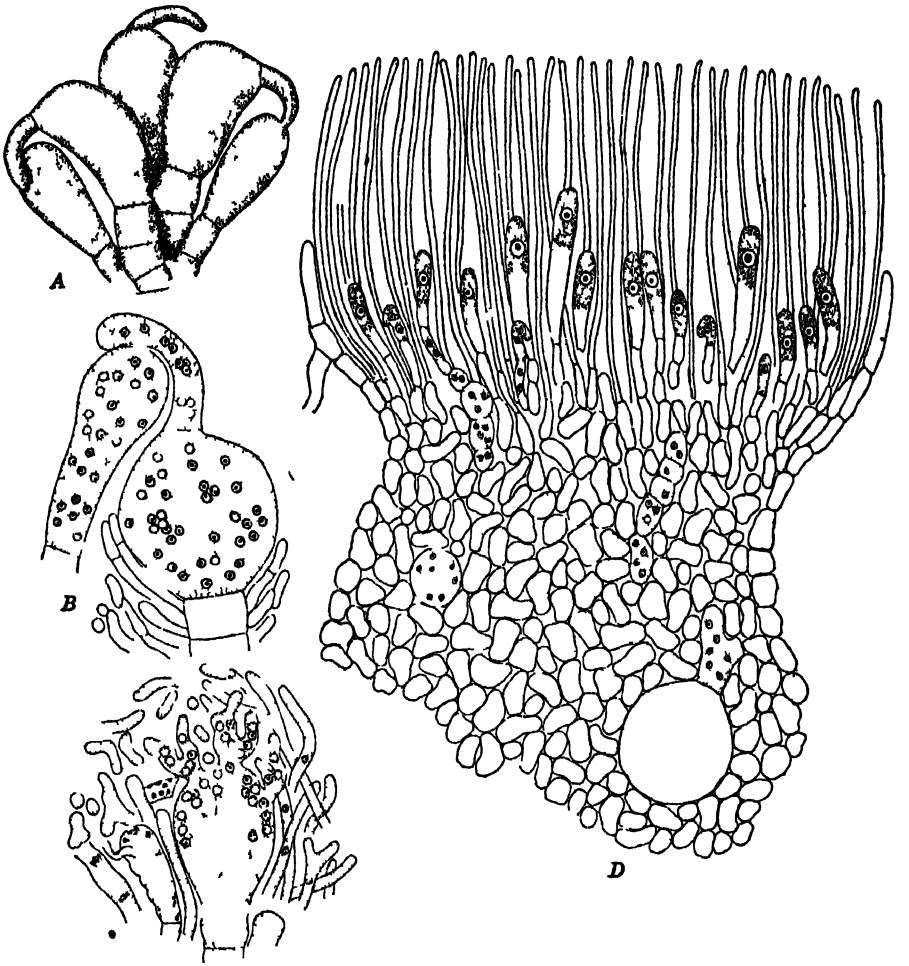


FIG 248 —*Pyronema confluens* (Pers) Tul *A*, surface view of a cluster of sex organs. *B*, vertical section of an apposed antheridium and ascogonium *C*, vertical section of an ascogonium with young ascogenous hyphae. *D*, diagrammatic vertical section of a young ascocarp. (*C*, *after Gwynne-Vaughan and Williamson*, 1931) (*A–B*, × 650; *C*, × 500; *D*, × 485.)

Pyronema is one of the saprophytic soil-inhabiting Pezizales. It is usually found growing only on soil that has been burned over, but it may grow in greenhouses or in seedbeds where the soil has been steril-

ized by steam.[1] The mycelium of *Pyronema* grows superficially on the soil and forms a white cottony layer. It is profusely branched and composed of relatively short cells, each with 6 to 12 nuclei.[2] There is no regular production of asexual spores, but certain erect hyphae of the mycelium may form chains of oïdia.[3]

Sexual reproduction begins four or five days after ascospores have been sown on a suitable substratum, and the ascocarps may be fully mature 10 days after the sowing of spores.[1] *P. confluens* (Pers.) Tul. is homothallic, and the mycelium developed from a single ascospore bears both antheridia and ascogonia.[4] At the time of sexual reproduction, a mycelium sends up dense tufts of short, erect, two- to four-celled branches in which the terminal cell of each branch is multinucleate and develops into an antheridium or an ascogonium (Fig. 248*A*). Cells developing into antheridia become club-shaped, and their nuclei divide and redivide until there are 100 or more. Those developing into ascogonia become subglobose and also come to contain a hundred or more nuclei (Fig. 248*B*). A developing ascogonium produces a curved, tubular, apical trichogyne whose tip grows toward, and becomes more or less curved about, the upper end of an antheridium. Later on, but still before fertilization, a transverse wall is formed across the base of the trichogyne. This is soon followed by a dissolution of cell walls in the region of contact between antheridium and trichogyne, a disintegration of nuclei in the trichogyne, and some disintegration of the central pore in the transverse wall between trichogyne and ascogonium. Most of the cytoplasm and a majority of the nuclei in an antheridium then flow into the ascogonium. The wall between trichogyne and ascogonium is reformed after this gametic union. Fusion of male and female nuclei in pairs has been affirmed[5] and denied,[6] but, taken as a whole, the evidence seems to show that there is a union of gamete nuclei. Fertilization is followed by a development of several irregularly branched tubular outgrowths (ascogenous hyphae) from the ascogonium (Fig. 248*C*). A majority of them develop on the upper side of an ascogonium, and most of the cytoplasm and a large majority of the nuclei migrate from the ascogonium into the hyphae. Young ascogenous hyphae are without cross walls: older ones are transversely septate and with binucleate cells toward the distal end. Each hyphal branch producing an ascus recurves to form a typical crozier in which the ascus is formed from a binucleate penultimate cell (Fig. 231). Ascus development takes place in the usual manner, with a union of the two nuclei, a formation of eight daughter nuclei from the fusion nucleus, and a cutting out of an ascospore about each nucleus.

[1] Seaver, 1909. [2] Claussen, 1912; Harper, 1900.
[3] L. R. and C. Tulasne, 1865. [4] Gwynne-Vaughan and Williamson, 1931.
[5] Harper, 1900; Gwynne-Vaughan and Williamson, 1931; Tandy, 1927.
[6] Claussen, 1912; Dangeard, 1907; Moreau and Moreau, 1930.

Numerous sterile branched hyphae develop from the cells below the ascogonium immediately after gametic union. These soon form a loosely interwoven envelope surrounding and overarching the united sex organs. The sterile hyphae enclosing one pair of united sex organs also become intertwined with those about adjoining pairs of sex organs. Thus several young apothecia become united to form a single compound one that is some 2 mm. in diameter at maturity. The apothecium of *Pyronema* is not as markedly cup-shaped as is that in most other Pezizales. However, the concave fertile layer of vertically parallel asci and sterile hyphae (paraphyses) is quite characteristic of the order (Fig. 248*D*).

Ascospores of *Pyronema* are capable of germination immediately after they are formed, but they may remain viable for a year or more if conditions are unfavorable for germination. The nucleus of a germinating spore divides to form six or more daughter nuclei; then the spore sends out one or two stout multinucleate hyphae [1] Each hypha soon becomes transversely septate and with 6 to 12 nuclei in the cytoplasm between two successive septa.

ORDER 6. TUBERALES

The Tuberales are wholly or almost wholly subterranean in habit and with an ascocarp that is a completely or an incompletely closed apothecium. The palisade-like layer of asci (hymenium) may be simple and surround a large central cavity within the apothecium, or the hymenium may lie in irregular folds that completely fill the central cavity. The order contains some 25 genera and 250 species.

Several genera are of widespread distribution in Europe. Truffles, the most highly prized of all edible fungi, include certain species of the genus *Tuber*, especially *T. melanosporum* Vittard. The gathering of truffles is a regular industry in France where the output for the year 1933 had a total value of 13,600,000 francs.[2] Truffles are not evident to those collecting them because they grow 3 to 12 inches below the surface of the soil. The gatherer of subterranean truffles locates them by their very characteristic odor. This is not evident to most human beings but is readily evident to many animals. The professional collector for the market trains dogs or pigs to locate truffles by scent and digs them up after the animal has discovered soil in which they are growing. Most of the Tuberales known from this country have been found in California.[3] Many of the species found in California are edible, but they have not been found in sufficient abundance to make their collection commercially profitable.

The thallus of *Tuber* is a colorless subterranean mycelium composed of numerous branching hyphae with short uninucleate cells. The hyphae

[1] Gwynne-Vaughan and Williamson, 1931.

[2] France, Ministere de l'Agriculture, 1935. [3] Gilkey, 1916; Harkness, 1899.

may run in all directions or may lie parallel to one another in thick strands (*rhizomorphs*). The mycelium of *T. melanosporum* seems to be a mycorhizal symbiont with roots of various trees, especially oaks and beeches.[1] Mycelia of other species, including *T. candidum* Harkn., are true saprophytes.

The only type of spore known for any of the Tuberales is the ascospore. There have been but few observations on early development of the

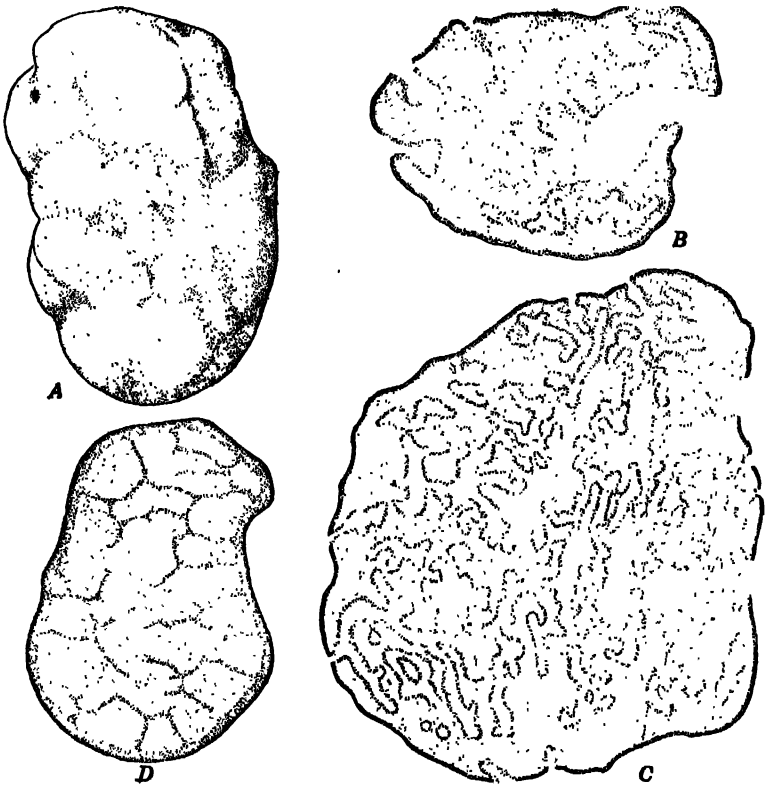


FIG. 249.—*Tuber candidum* Harkn. *A*, surface view of a mature ascocarp. *B–C*, sections of young ascocarps. *D*, vertical section of a mature ascocarp. (*A*, × 2; *B–C*, × 9; *D*, × 3.)

ascocarp and in no case has it been found young enough to show the sex organs. Young ascocarps of *Tuber* are apothecia in which there is an early differentiation of the parallel multicellular paraphyses of the hymenial layer. This layer is irregularly folded in the young ascocarp, and, as development continues, the folding becomes more and more pronounced (Fig. 249*B–D*). The interstices between opposite folds of the hymenium are filled with a loosely interwoven mass of hyphae thought to be formed by an outgrowth of certain of the paraphyses.

[1] Dangeard, 1894.

In *T. candidium* formation of the hymenium seems to be preceded by a localized pulling away from one another of hyphae within the thallus. This results in linear cavities containing very loosely interwoven hyphae (Fig. 250*A*). Many newly formed hyphal branches then grow toward the cavity and become arranged in a palisade-like layer encircling it. The ascogenous hyphae may be recognized by their greater breadth and their denser protoplasts (Fig. 250*A*). They lie just below the palisade-like paraphyses, and their tips are recurved to form croziers in which the penultimate binucleate cell develops into an ascus.[1] The two nuclei

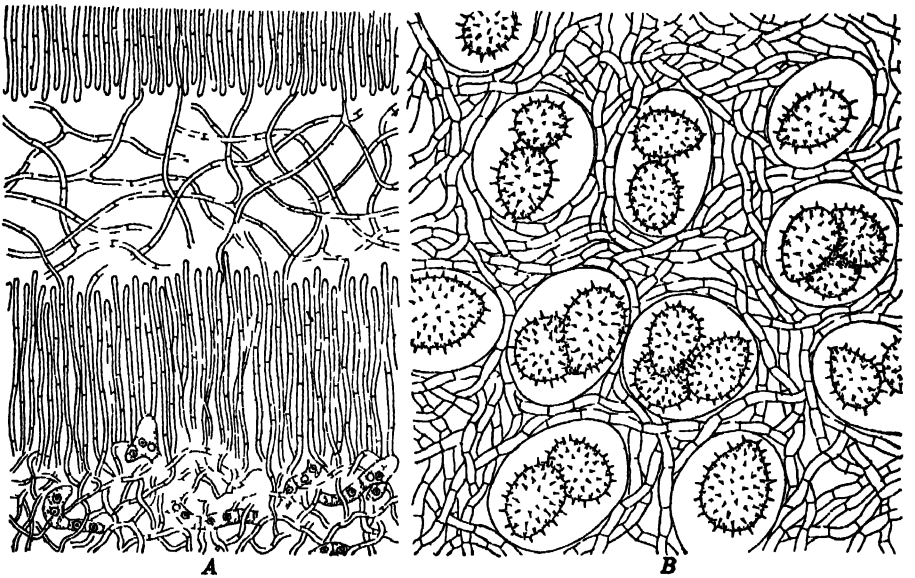


FIG. 250.—*Tuber candidum* Harkn. *A*, young ascogenous hyphae beneath the hymenial layer. *B*, portion of the fertile region of a mature ascocarp. (*A*, × 650; *B*, × 430.)

in a young ascus unite with each other, and the fusion nucleus divides to form eight daughter nuclei.[2] Ascospores are cut out around certain of the nuclei only (Fig. 251). In *T. candidum* the number of spores in a mature ascus ranges from one to seven (Fig. 250*B*). Ascospores of *Tuber* have the spore wall ornamented with spines or with reticulations.

A mature ascocarp (Fig. 249*A*) is more or less globose, has a smooth or warty surface, and is rarely more than 8 cm. in diameter. The outer portion of the ascocarp is a sterile thick-walled tissue known as the cortex. In certain parts of an ascocarp the cortex is derived from the outer region of the young apothecium; in other parts of the ascocarp it is derived from the ascogenous tissue. An ascocarp remains unopened after it is fully mature, and the ascospores are only liberated by a decay

[1] Schussnig, 1921. [2] Dangeard, 1894; Schussnig, 1921.

of the cortex. Spore dispersal may be effected through the agency of animals, especially rodents. In California, certain of the Tuberales are a favorite food of wood rats[1] which detect them by means of their very characteristic odor. The ascocarp dug up by the rat may either be eaten on the spot or carried to its burrow. In either case, crumbs falling on the ground may inoculate the soil Spore dispersal may also

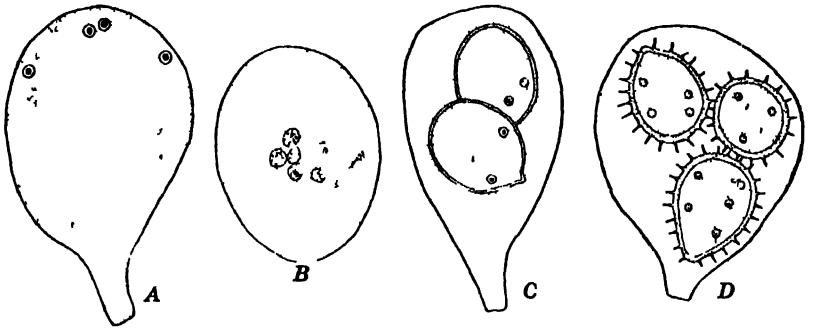


FIG. 251 —*Tuber candidum* Harkn *A*, young ascus *B*, ascus just after the formation of an ascospore *C D*, young and mature ascospores. (× 650)

be effected by undigested ascospores passing through the alimentary tract of an animal that has eaten an ascocarp [2]

ORDER 7. HELVELLALES

The Helvellales have a sessile or stalked ascocarp with a freely exposed, smooth or wrinkled, everted ascogenous layer in which the asci are parallel to one another The order contains some 275 species, almost all of which are soil-inhabiting saprophytes

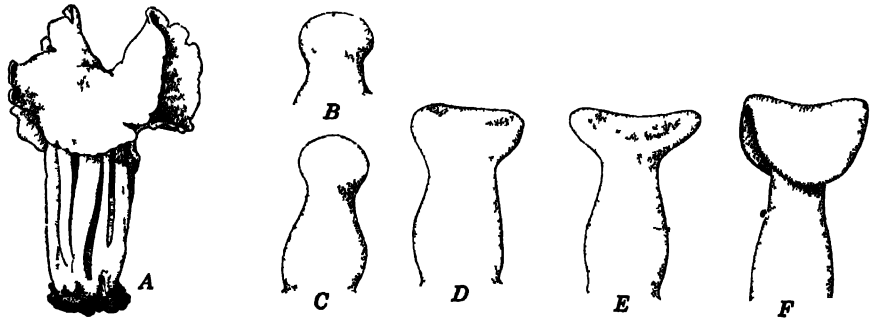


FIG. 252 —*A*, mature ascocarp of *Helvella crispa Fries* *B F*, *H elastica* Bull, early stages in development of an ascocarp. (*B–F, after McCubbin*, 1910) (*A*, × ½, *B–E*, × 5½, *F*, × 3½)

Helvella has a much-branched subterranean mycelium of many loosely interwoven multicellular hyphae in which each cell contains 2 to 16 nuclei.[3] There are numerous anastomoses between the various

[1] Parks, 1919 [2] Massee, 1909 [3] McCubbin, 1910.

hyphae. The mycelium of *Helvella* has never been found producing asexual spores, but that of a closely related genus has been found with conidia.[1]

Sex organs have never been found in young ascocarps. This may be due to the fact that they have been overlooked. There is also the possibility that the production of sex organs has been replaced by a fusion of nuclei in pairs in certain of the vegetative cells. This nuclear fusion has been described[2] for vegetative cells of *H. crispa* Fries but cannot be accepted unreservedly since the observed pairing might have been due to a recent division of, rather than to a fusion of, nuclei. The portion of a mycelium developing into an ascocarp is composed of hyphae that are shorter, thicker, and more profusely branched.[3] Young asco-

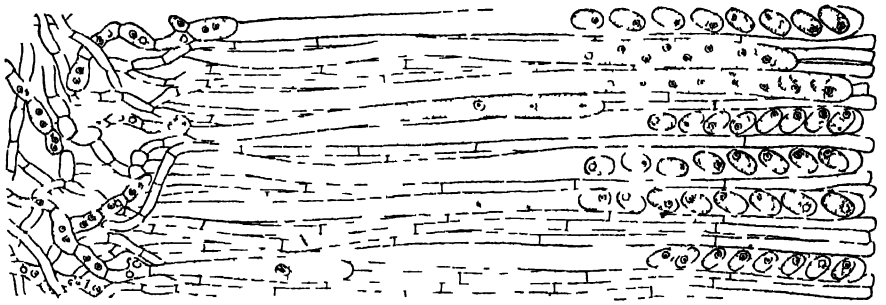


FIG. 253.—*Helvella* sp. Diagrammatic vertical section of a portion of the hymenium showing asci at various stages of development. (× 325.)

carps of *H. crispa*, approximately 0.5 mm. in diameter, consist of a stout stem and a bulbous cap of somewhat greater diameter (Fig. 252*B–C*). At this stage there is no differentiation of tissues within the cap. Soon after this there is the formation of a palisade-like layer of parallel hyphae over the surface of the cap. Certain of the hyphae grow beyond the palisade layer and interlace with one another to form a thin overlying layer that disappears as the cap develops further. The palisade region of the cap grows more rapidly than does the region internal to it. As a result, the cap soon assumes the saddle-shape form characteristic of the mature fruiting body of *H. crispa* (Fig. 252*D–F*). Young ascocarps are subterranean, but, as they grow older, they push up through the soil and the above-ground portion eventually attains a height of 2 to 8 cm. (Fig. 252*A*).

The ascogenous hyphae are first evident while the ascocarp is subterranean and about 1 mm. in diameter. They lie in a matted web parallel to and a short distance below the palisade layer.[3] Ascogenous hyphae have a breadth twice to thrice that of other hyphae. The matted web of ascogenous hyphae sends out upright branches that grow toward

[1] Molliard, 1904. [2] Carruthers, 1911. [3] McCubbin, 1910.

the palisade layer, where they branch repeatedly. The tips of these latter branches become recurved to form typical croziers in which the penultimate binucleate cell develops into the ascus.[1] The two nuclei in a young ascus unite with each other, and the fusion nucleus divides to form eight daughter nuclei. An ascospore is delimited about each nucleus, and the eight ascospores within a mature ascus lie in a linear series (Fig. 253).

There is an explosive discharge of the ascospores when they are liberated from an ascus. The period of spore discharge may last for several days because all asci do not mature at the same time.[2] *Helvella* is one of the ascomycetes in which "puffing" has been observed,[2] and discharge of ascospores is accompanied by a distinctly audible hissing sound.

ORDER 8. EXOASCALES

The Exoascales have asci that lie parallel to one another in a palisade-like layer that is without any enclosing peridium. The order contains less than a hundred species, all of them parasitic. The present tendency is to group all species in the genus *Taphrina*, instead of recognizing two or three additional genera, including *Exoascus*.

Two of the species, *T. deformans* (Fcl.) Tul. and *T. Pruni* (Fcl.) Tul., cause serious diseases of orchard trees. The former produces a leaf curl of peaches (Fig. 254*A*), the latter a malformation of plum fruits.

Germinating spores of certain species give rise to a mycelium that has binucleate cells from the beginning.[3] Those of certain other species give rise to a mycelium of uninucleate cells which become binucleate during the course of vegetative growth.[4] The mycelium in parenchymatous tissues of leaf and stem is intercellular. In some species, as *T. deformans*, it is almost wholly confined to tissues developed in the current year; in other species, as *T. Pruni*, it is perennial and invades new twigs and leaves developed in the spring. There is no formation of asexual spores by the mycelium.

Prior to ascus formation most species develop a compact, parenchymatous, mycelial layer, one cell in thickness, between cuticle and epidermis of the host. According to the species, this layer develops on the leaf or on the fruit. All cells of the layer are binucleate, and in each of them the two nuclei fuse as the cell elongates vertically. A few species, including *T. carnea* Johans.,[5] have the cells with fused nuclei developing directly into asci. A majority of the species have each of these cells dividing into a short stalk cell and a sister cell that develops into the

[1] McCubbin, 1910; Carruthers, 1911. [2] DeBary, 1887.
[3] Eftimiu, 1927; Fitzpatrick, R. E., 1934; Wieben, 1927.
[4] Martin, 1924. [5] Juel, 1921.

ascus (Fig 254*B*) In *T Coryli* Nishida the stalk cell and ascus each contain a single daughter nucleus formed by a heterotypic division of the fusion nucleus [1] The nucleus in the stalk cell degenerates; that in the ascus divides and redivides equationally to form eight daughter nuclei Eight ascospores are then formed, and they are surrounded by a certain amount of epiplasm Almost all other species also have asci with eight ascospores In certain cases the nuclear divisions preceding ascospore formation have been shown [2] to be reductional

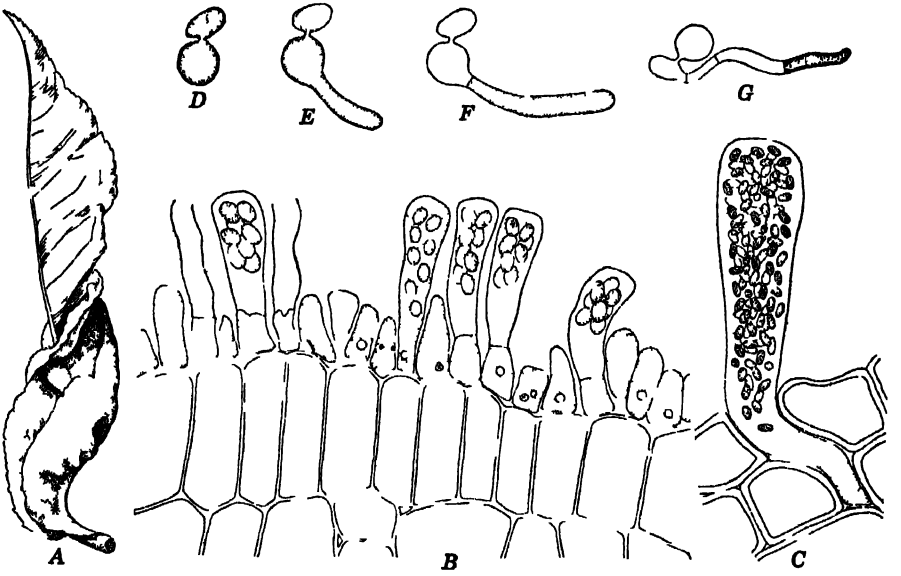


FIG 254 *A B Taphrina deformans* (Berk) Tul 1 an infected peach leaf showing the characteristic malformation *B* asci at various stages of development *C I Johansonii* Sadeb ascus containing many conidia *D G I epiphylla* Sadeb stages in the conjugation of conidia and the formation of hyphae (*D G after Wieben* 1927) (*A*, × $\frac{1}{2}$ *B C* × 650)

Ascospores may be discharged from an ascus without germinating (*T deformans*), or they may germinate to form a number of conidia while still within the ascus (*T Johansonii* Sadeb) Conidium formation resembles the budding of yeasts, and the first conidium budded off may bud off a succession of conidia (Fig 254*C*) Spores of *T deformans* frequently bud off a series of conidia immediately after they are liberated from an ascus [3] Ascospores of *T deformans*, or conidia derived from them, lodging on twigs and branches infect the young leaves as they unfold the next spring [4] The hypha produced by a germinating ascospore or conidium grows directly through the cuticle and between epidermal cells of the host The single nucleus in the spore divides into two

[1] Marin, 1924 [2] Juel, 1921 [3] Martin, 1925, Mix, 1924
[4] Fitzpatrick, R E, 1934

daughter nuclei, and they divide conjugately into pairs of daughter nuclei. Transverse wall formation between the pairs of nuclei results in a binucleate mycelium. Certain other species also have nuclear division in the budding ascospore initiating the binucleate phase of the life cycle.[1]

At least two species of *Taphrina* are heterothallic. In these species a conjugation tube is formed between a pair of ascospores or conidia, and the protoplast of one spore migrates through it into the other spore (Fig. 254*D–G*). The binucleate protoplast thus formed then develops into a mycelium in which all cells are binucleate.[2] Conjugation may even take place between spores of the same ascus since four of them are plus and four are minus.

The systematic position of the Exoascales is a matter of dispute. Some[3] consider them simpler than ascomycetes with a definite ascocarp. If the Exoascales are primitive, they stand at a higher level than the Protoascomycetae because the asci are not developed directly from what corresponds to gametangia. Others[4] consider them reduced from ancestors that produced definite ascocarps and presumably one of a discomycete type. This interpretation seems the more probable. The entire mycelium of *Taphrina* with its binucleate cells is the equivalent of the ascogenous hyphae in a discomycete.

ORDER 9. HYPOCREALES

The Hypocreales have an ascocarp that is a perithecium and one with a periderm that is light colored, soft in texture, and distinct from the remainder of the mycelium. A perithecium may stand above or be embedded in the mycelium. The order includes more than 60 genera and 1,750 species.

Claviceps is a genus parasitic on ovaries of Gramineae. During the course of development of the fungus, the ovary is replaced by a dark-colored compacted mass of fungus tissue, the *sclerotium* (Fig. 256*A*). The sclerotium of *Claviceps* is called *ergot*. There are a dozen or more species, the most important of which is *C. purpurea* (Fries) Tul, parasitic on rye and on several wild grasses. *C. purpurea* rarely causes an appreciable diminution in the yield of rye. On the other hand, a relatively small percentage of ergot bodies in the harvested grain produces a serious physiological disease, known as ergotism, when the grain is used as food by man or domestic animals. Ergotism was fairly common among the people of Europe during the Middle Ages, but it has been greatly

[1] Martin, 1936. [2] Wieben, 1927.

[3] Schröter, Lindau, and Fischer, 1894–1897; Gaumann and Dodge, 1928; Juel, 1921.

[4] Bessey, 1935; Gwynne-Vaughan and Barnes, 1927.

diminished in recent times on account of the introduction of modern methods of milling grain. Even today ergotism has not completely disappeared, and within the past decade there has been a mild epidemic in England and a severe one in Russia among consumers of rye bread.[1] Epidemics of ergotism among animals are chiefly in cattle grazing on grasslands badly infected with *Claviceps*. Ergot is an officially recognized drug that is used as an abortifacient and to control hemorrhage during childbirth. The active ingredients in ergot are alkaloids.

Infection of the host takes place only at the time of flowering and the region of infection seems to be restricted to the pistil. Hyphal branches developing from the spore soon invade and destroy the ovule, replacing it with a soft mycelial mass of much the same shape. The peripheral portion of the mycelial mass becomes greatly convoluted and there is a development of a palisade-like layer of short conidiophores over the entire surface.[2] Minute ovoid uninucleate conidia are cut off in acropetalous succession at the tip of each conidiophore (Fig. 255). These constitute the *Sphacelia* stage in the life history, so-called because the conidia were once considered an imperfect fungus, *Sphacelia segetum* Lév. The conidia accumulate in a sweetish liquid exuding from the spikelet. This liquid, "honeydew," is eaten greedily by various insects, and there may be a certain amount of reinfection as an insect travels from flower to flower and plant to plant. The conidia remain viable during the winter[3] so that it is possible for them to infect flowers developed the next summer. Eventually the basal region of the hyphal mass ceases to produce conidia and develops into a densely compacted dark-colored tissue. This is followed by a progressively upward metamorphosis into compact tissue until the whole mycelium has been changed into a sclerotium that is capped with remnants of the sphacelial tissue. Mature sclerotia are considerably longer and broader than the normal grains in panicles of the Gramineae.

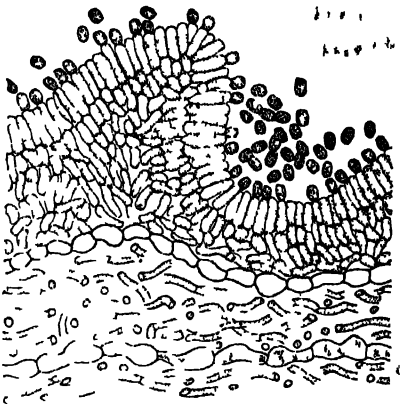


FIG. 255.—Sphacelial stage of *Claviceps purpurea* (Fries) Tul. (× 650.)

Maturation of sclerotia coincides with ripening of the grains in a panicle. Some of the sclerotia on a panicle of rye fall to the ground; others become intermingled with the grain when rye is harvested and threshed. These may be returned to the same field or to other fields when a new crop of rye is sown. Sclerotia may also be dispersed by

[1] Dixon, 1932. [2] Tulasne, 1853. [3] Stager, 1912.

other agencies than man. In certain grasses the sterile portions of an infected flower mature into the barbed awns that effect a dispersal of normally developed grains of the species. Sclerotia of most grasses sink in water.[1] Those of grasses growing in marshes or along the banks of streams are often buoyant in water and thus may be transported some distance from the plant on which they developed

Overwintering sclerotia that have not lost too much moisture produce perithecia the next spring. The relation between water content and

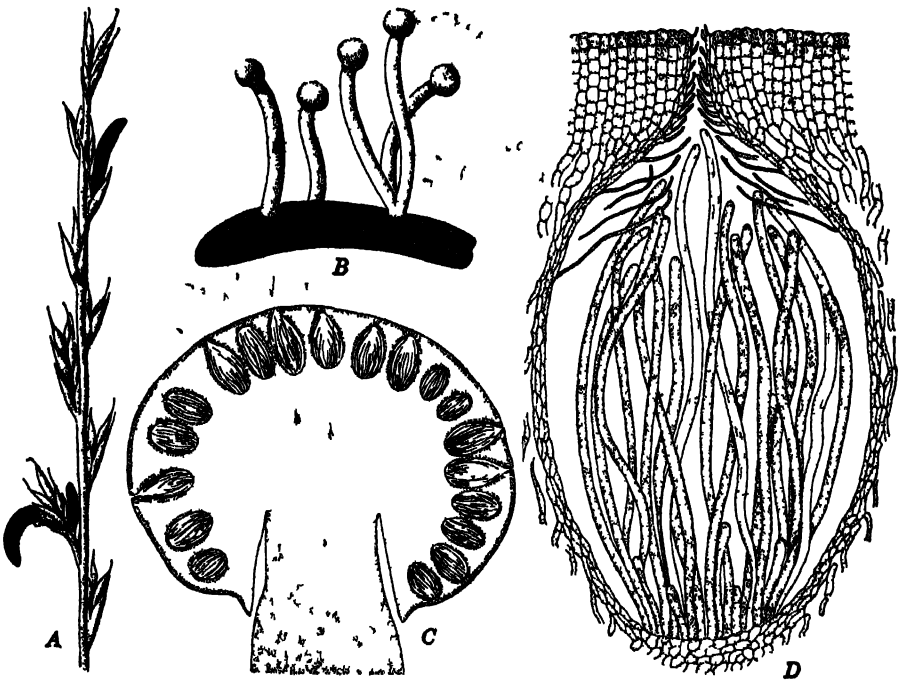


FIG 256.—*Claviceps purpurea* (Fries) Tul. *A*, panicle of *Agropyron repens* (L.) Beauv. with sclerotia of *Claviceps*. *B*, germinating sclerotium. *C* vertical section of a fruiting stroma. *D*, semidiagrammatic vertical section of a perithecium. (*A*, natural size, *B*, × 4, *C*, × 60, *D*, × 480.)

viability becomes quite evident when sclerotia are brought into the laboratory. Sclerotia placed on moist sand soon after they are brought into the laboratory eventually germinate; those kept air-dry until spring and then placed on moist sand rarely germinate. A germinating sclerotium produces a half dozen or more small capitate outgrowths borne on stalks 10 to 20 mm. long (Fig. 256*B*). The capitate portion (stroma) of each outgrowth contains many perithecia (Fig. 256*C*). Certain branched hyphae somewhat below the surface of a stroma produce the sex organs. These hyphae may be distinguished from others on account of their

[1] Stäger, 1922.

richer protoplasmic content.[1] Antheridia and ascogonia are produced on the same hypha, each developing from the terminal cell of a lateral branch. Cells developing into sex organs soon become multinucleate, and those developing into ascogonia become broader than those developing into antheridia. An ascogonium develops a small lateral outgrowth that becomes applied to an antheridium. The cell walls dissolve in the region of mutual contact, and the nuclei of the antheridium migrate into the ascogonium.[1] Ascogenous hyphae then grow from the ascogonium, and asci are formed at the tips of ascogenous hyphae bent into typical croziers.

The asci are produced in perithecia so deeply sunken in adjoining stromatic tissue that only the opening (the ostiole) protrudes. Each ascus contains eight elongate acicular ascospores that lie parallel to one another (Fig. 256*D*). The ascospores are forcibly discharged from an ascus, but this only takes place when a perithecium is vertically upright. At the time of spore discharge the stalk below the fertile head slowly twists and turns. As a result, every perithecium of the stroma is vertically upright for a short time.[2] Ascospores are ejected with a force sufficient to hurl them 20 to 80 mm.[3] Convection air currents may then carry the spores to the flowering head of rye, or the spores may be transported some distance by winds.

ORDER 10. SPHAERIALES

The Sphaeriales have an ascocarp that is a perithecium and one in which the peridium is dark colored and distinct from the rest of the mycelium. A perithecium may stand above or be embedded in the mycelium. The order includes some 275 genera and 11,000 species.

Venturia is a parasitic genus with about 50 species. From the economic standpoint, the most important of these is *V. inaequalis* (Cooke) Wint. which causes apple scab (Fig. 257). Both the leaf and the fruit of the host may be infected, and, when infection is severe, the yield of marketable fruit may be reduced 50 per cent or more.

The early spring infection of young leaves and blossoms is usually by means of ascospores developed on dead leaves of the previous year. In regions with a mild climate, as California, infection may be caused by overwintering conidia. An ascospore falling on a leaf sends out a germ tube that grows directly through the cuticle and then grows between the cuticle and epidermis. The hypha soon develops into a radiately branched mycelium of uninucleate cells that lies entirely between cuticle and epidermis.[4] Within a short time the subcuticular mycelium becomes a brownish layer more than one cell in thickness, and one in which the

[1] Killian, 1919. [2] Whetzel and Reddick, 1911.
[3] Falck, 1910. [4] Wallace, 1913.

uppermost cells develop into conidiophores (Fig. 258*A*). Formation of conidia at the distal end of the conidiophores is accompanied by a rupture of the overlying cuticle. The conidia of the acervulus thus exposed become detached from the conidiophores immediately after they are formed. Conidiophores produced on the host never show the chains of conidia that are sometimes present when the fungus is grown in artificial culture.[1] Conidia scattered to other parts of the tree or to other trees germinate to form mycelia that produce further conidia, also capable of reinfecting the host, and this asexual reproduction continues until abscission of leaves and fruits. For a long time this was the only known method of reproduction, and the fungus was placed among the Imperfecti and called *Fusicladium dentriticum* (Wallr.) Fcl.



FIG. 257.—Apples infected with *Venturia inaequalis* (Cooke) Wint. (*Photograph by G. W. Keitt*)

Eventually there was a demonstration[2] that it is the conidial stage of a pyrenomycete, *Venturia*.

Development of the perithecial stage is preceded by a shift from a parasitic to a saprophytic mode of nutrition and one in which food is obtained from the decaying leaves or fruits of the host. When the fungus is parasitic, it grows only between cuticle and epidermis of the host; with death and decay of the leaf or fruit, hyphae grow out from the subcuticular layer and penetrate the disintegrating underlying host tissues. Sex organs are produced on these hyphae late in the autumn. A development of perithecia also takes place when the fungus is grown in culture if the temperature is a few degrees above the freezing point.[1] *Venturia* differs from most other ascomycetes in that the peridium of the ascocarp begins to develop before instead of after fertilization. Perithecial development begins with a coiling about each other of two unicellular branches from the same hypha. Cell division in each branch soon brings about the formation of a solid spherical mass of cells. With further development of this young globose perithecium, there is a differentiation of a long, coiled, multinucleate ascogonium. The distal end of

[1] Frey, 1924 [2] Aderhold, 1894.

the ascogonium, the trichogyne, protrudes beyond the surrounding sterile cells. One or more hyphae arising in the vicinity of a young perithecium grow toward the trichogyne, and their apical cells become applied to it. The apical cell of such a hypha is an antheridium. It is generally bulbous in shape and with more than one nucleus. After a dissolution of apposed walls, the nuclei in the antheridium migrate into the trichogyne and down to the ascogonium. After this the ascogonium becomes transversely septate (Fig. 258 *B*) and most of the cells thus formed are binucle-

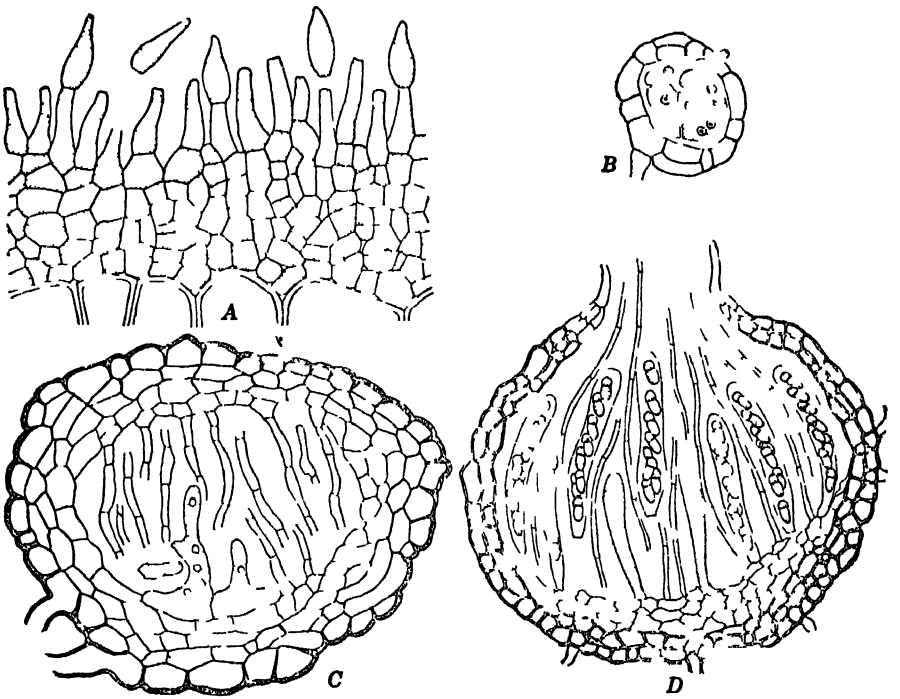


FIG. 258 *Venturia inaequalis* (Cooke) Wint *A* conidia. *B*, ascogonium. *C*, young perithecium with ascogenous hyphae *D*, mature perithecium. (*A–C*, × 650, *D*, × 325.)

ate. One or more of the cells formed from the ascogonium now send out ascogenous hyphae (Fig. 258*C*) from the upper side.[1] The ascogenous hyphae are branched, are transversely septate, and have the tips developing into typical croziers in which the binucleate penultimate cell becomes an ascus. The fusion nucleus in an ascus divides to form eight daughter nuclei, and eight ascospores are delimited in the usual manner. Each ascospore forms a single transverse septum before spore discharge.

Mature perithecia (Fig. 258*D*) are flask-shaped and with a dark-colored peridium. Maturing perithecia have a disintegration of certain cells in the upper portion of the peridium to form an ostiole. In mature

[1] Killian, 1917.

perithecia it is encircled by a ring of unicellular bristles. Asci in mature perithecia elongate until their tips project through the ostiole. Protrusion of an ascus through the ostiole is followed by an ejection of ascospores with sufficient force to hurl them to a height of 10 mm.[1] Discharge of ascospores may continue for a month or more since neither all asci in a perithecium nor all perithecia on a dead leaf mature simultaneously. The period of spore discharge synchronizes with flowering of the host. In areas with an early spring, as the Pacific Coast states and Virginia, the ascospores are discharged in late February and early March, but in areas where spring is late, as Wisconsin and Vermont, most of the ascospore discharge is in May. In all areas spore discharge is closely correlated with weather conditions, and most of it takes place immediately after a rain.

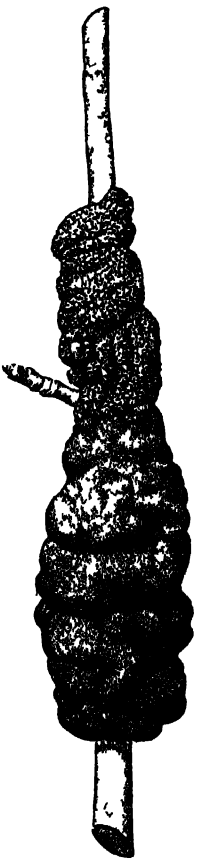


FIG. 259.—A young branch of a cherry tree infected with *Plowrightia morbosa* (Schw.) Sacc. (×¾)

ORDER 11. DOTHIDIALES

The Dothidiales have an ascocarp that is a perithecium and one in which the peridium is not distinct from the remainder of the mycelium. The perithecia are embedded in the mycelium. The order includes about 130 genera and 1,200 species.

Plowrightia is a parasitic genus with some 35 species. The best-known of these is *P. morbosa* (Schw.) Sacc. that produces conspicuous galls (black knot) on branches of cherries and plums (Fig. 259). Infection of the host takes place during the spring and upon twigs of the current year's growth or upon those not over two or three years old. The mycelium does not produce spores until the following year. During the first year the cambial cells in an infected area of the host divide more rapidly than those in uninfected portions.[2] Only a relatively few of the cells cut off toward the internal face of the cambium mature into wood. On the other hand, there is an increased production of parenchyma internal to the cambium and opposite wood rays more than one cell broad (multiseriate rays). The portion of each multiseriate ray formed after infection is very much broader and has the appearance of a compound ray. At the end of the first growing season the infected portion of a branch or twig is externally recognizable as a slight swelling.

When the host resumes growth the next spring, there is a very rapid swelling of the diseased area. The overlying bark soon ruptures and

[1] Wallace, 1913. [2] Stewart, 1914.

hyphae growing from the exposed cortex begin to develop into a dense pseudoparenchymatous tissue. The whole surface of this tissue becomes covered with a velvety layer of simple or branched septate filaments. These are conidiophores, and at or near the tip of each of them there are one or more small ovoid conidia[1] (Fig. 260*A*). Conidia inoculated onto other individuals of the host produce typical infections.[2] The velvety layer of conidiophores disappears toward midsummer, and the underlying dense mycelial tissue becomes dead black and of a hard, brittle texture.

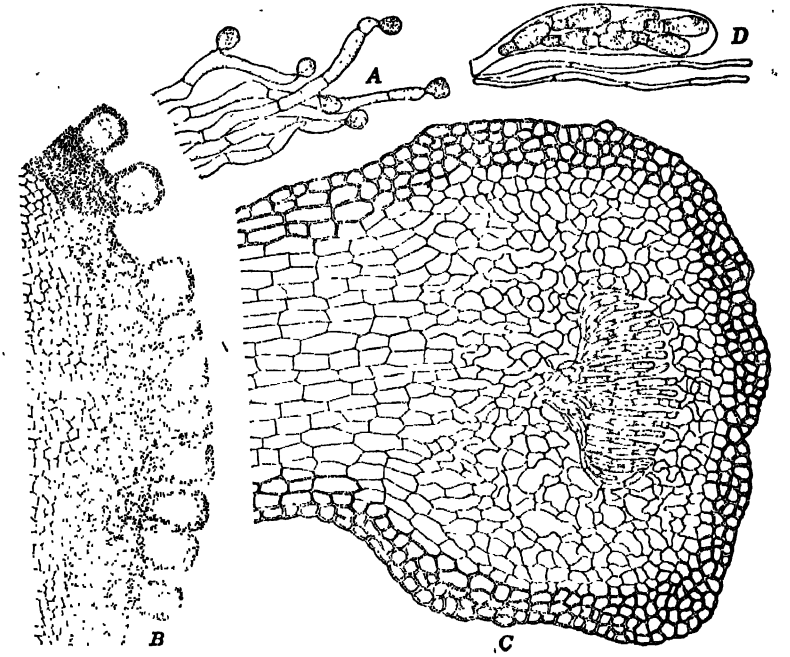


FIG. 260.—*Plowrightia morbosa* (Schw.) Sacc. *A*, conidia. *B*, transverse section of stroma bearing young perithecia. *C*, vertical section of a young perithecium in which there are sterile paraphyses in the region where asci will be formed. *D*, ascus. (*A*, *D*, × 650; *B*, × 30; *C*, × 325.)

There is considerable uncertainty as to whether asexual reproduction by conidia is followed by a formation of pycnospores. Three types of pycnidia have been found[3] in the black stroma of *P. morbosa*, but at least one of these belongs to a saprophytic or parasitic fungus growing on the stroma. On the other hand, there has been a production of pycnidia in cultures of a mycelium derived from the germination of an ascospore.[4]

Perithecial development begins shortly before disappearance of the conidiophores, and several perithecia are formed in a stroma (Fig. 260*B–C*).

[1] Farlow, 1876; Humphrey, 1891. [2] Gilbert, 1913.
[3] Farlow, 1876. [4] Humphrey, 1891.

The details of perithecial development have not been described. Mature perithecia are obovoid, with a small ostiole, and with a peridium that is not distinct from the remainder of the stroma. Asci are developed during the following winter.[1] They contain eight ascospores, each with a single transverse septum (Fig. 260*D*). Ascospore liberation takes place early in the spring, and typical infections have been obtained when twigs of the host are inoculated with ascospores.[2]

ORDER 12. LABOULBENIALES

The Laboulbeniales are minute ectoparasites on the cutinous integuments of living insects. All genera have an ascogonium with a trichogyne and one in which fertilization is effected by means of spermatia. The mature asci lie within a small perithecium. The order includes some 50 genera and 1,250 species.

Reproductive structures of the Laboulbeniales bear a closer resemblance to analogous structures of Rhodophyceae than do those of any other ascomycete. Because of this, those who think that the Ascomycetae originated among the red algae consider the Laboulbeniales the most primitive of all Ascomycetae. On the other hand, Laboulbeniales must be ranked among the more advanced ascomycetes if one follows those who think that fertilization by means of spermatia was evolved after the ascomycetes had become a well-established series. Their relationship to other advanced orders is obscure because of the extensive modification of the thallus in connection with adaptation to existence upon a motile host that is not injured by presence of the parasite.

Stigmatomyces Baeri Peyritsch is relatively simple in structure as compared with many other Laboulbeniales. It grows upon the European house fly (*Musca domestica* L.). The fungus may be attached to any part of the fly, but more commonly it grows on the back of the head and thorax or upon the anterior pair of legs.[3] Infection of the host is only by means of ascospores. An ascospore is broadly acicular, transversely divided into two cells, and with a gelatinous envelope that is characteristically thickened at one pole (Fig. 261*A*). The sticky envelope about a spore facilitates adherence when the basal end of a spore becomes attached to the host. Shortly after attachment to the host, the lower cell cuts off a short dark-colored foot cell (Fig. 261*B*). The uppermost cell of this three-celled stage eventually develops into the appendage bearing the antheridia and subtending parts; the median cell develops into the perithecium and subtending parts; the foot cell does not divide again and serves as an organ of attachment for the rest of the fungus.

Development of the antheridial portion begins with a succession of oblique divisions of the upper cell.[3] All daughter cells but the uppermost

[1] Farlow, 1876. [2] Gilbert, 1913. [3] Thaxter, 1896.

then divide in a plane perpendicular to the oblique wall (Fig. 261*C–F*). The upper daughter cell of each pair redivides transversely, and its superior daughter cell is metamorphosed into an antheridium (Fig. 261*H–I*). Each antheridium is flask-shaped, and, as it matures, there is a formation of an apical pore in the neck portion of the flask. The protoplast within an antheridium is uninucleate,[1] and it cuts off a minute

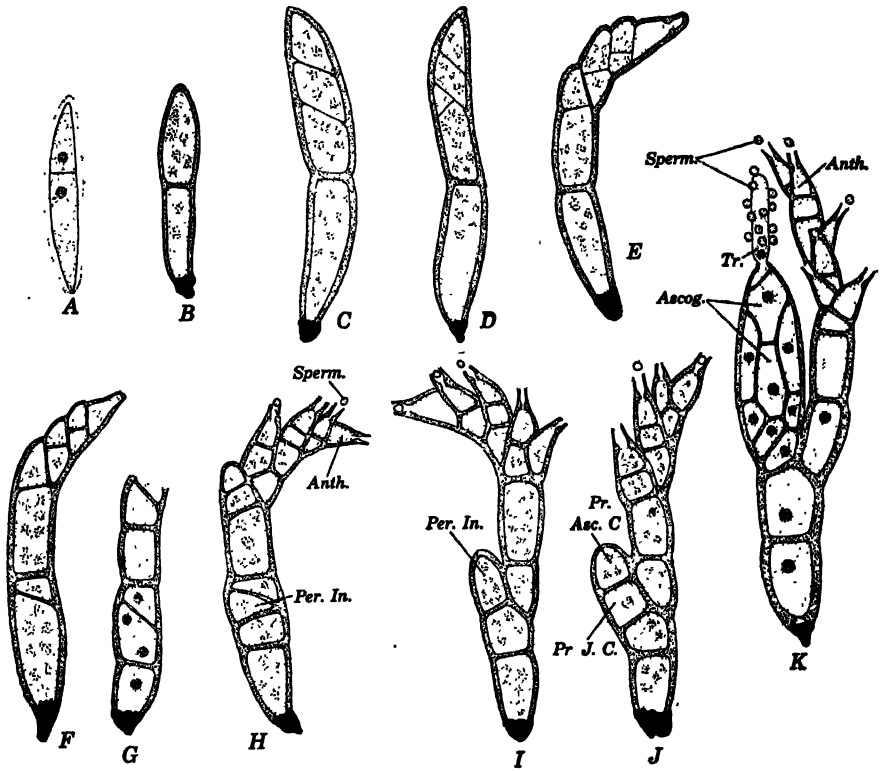


FIG. 261.—*Stigmatomyces Baeri* Peyritsch. Stages in development up to the time of ertilization. (*Anth.*, antheridium; *Ascog.*, ascogonium; *Per. In.*, perithecial initial; *Pr. Isc. C.*, primary ascogonial cell; *Pr. J. C.*, primary jacket cell; *Sperm.*, spermatium; *Tr.*, richogyne.) (*After Thaxter*, 1896.)

uninucleate protoplast (the spermatium) that escapes through the pore in the antheridial wall. Escape of the spermatium is followed by a formation and a discharge of a second one. This may be repeated many times.

The median cell of the three-celled stage does not divide until the antheridia are well along in development.[2] It divides by a diagonally transverse wall into a small superior cell (that does not divide) and a large inferior cell (Fig. 261*F*). The inferior cell divides transversely

[1] Faull, 1911. [2] Thaxter, 1896.

(Fig. 261*G*) and its upper daughter cell divides transversely. The two lowermost of the three cells formed by division of the inferior cell do not divide further; the uppermost one is the perithecial initial from which the entire perithecium is developed (Fig. 261*H–I*). The perithecial initial elongates outward from other cells of the young thallus and then divides transversely (Fig. 261*J*). The upper daughter cell produced by this division is the *primary ascogonial cell;* the lower daughter cell is the *primary jacket cell* of the perithecial jacket (peridium). The primary ascogonial cell develops into an ascogonium that is four cells long and one in which the uppermost cell is a trichogyne. It is very probable that nuclear fusion takes place in the lowermost cell of the ascogonium after spermatia have lodged on the trichogyne. Meanwhile, the primary jacket cell has developed into a perithecial jacket (Fig. 261*K*). Eventually this becomes two cells in thickness and several cells in perimeter.[1] After fertilization, short stout ascogenic cells grow out from the base of the ascogonium, and each ascogenic cell gives rise to several asci. The ascogenic cells of Laboulbeniales are homologous with the ascogenous hyphae of other Euascomycetae. Nothing is known concerning the cytology of ascogenic cells in *S. Baeri,* but it is known that they are binucleate in certain other Laboulbeniales.[2] In such Laboulbeniales the two nuclei divide conjugately, one pair of daughter nuclei migrating into an ascus budded off from the ascogenic cell, the other pair remaining in the ascogenic cell. This may be repeated several times. In the Laboulbeniales where ascus development has been studied,[2] the two nuclei in a young ascus unite with each other, and the fusion nucleus divides and redivides to form eight daughter nuclei. According to the genus, there is a formation of an ascospore about each nucleus or about four nuclei only. *S. Bayeri* is of the latter type.

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[1] Thaxter, 1896. [2] Faull, 1911, 1912.

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CHAPTER XIII

BASIDIOMYCETAE

The life cycle of a basidiomycete always includes the development of a special one- to four-celled structure—the *basidium*, upon which are borne a definite number (usually four) of *basidiospores*. Many members of the class produce one or more other types of spore in addition to basidiospores. There are more than 460 genera and 23,000 species of basidiomycetes. Fungi referred to the Basidiomycetae include the mushrooms and their allies (the hymenomycetes), the puffballs and their allies (the gasteromycetes), the smuts, and the rusts.

Vegetative Structure. The mycelium of a basidiomycete is always multicellular and freely branched. It may consist of a simple weft of hyphae; or, as in mushrooms and puffballs, a majority of the hyphae may be interwoven into a macroscopic body of definite form in which there is a considerable internal differentiation of tissue.

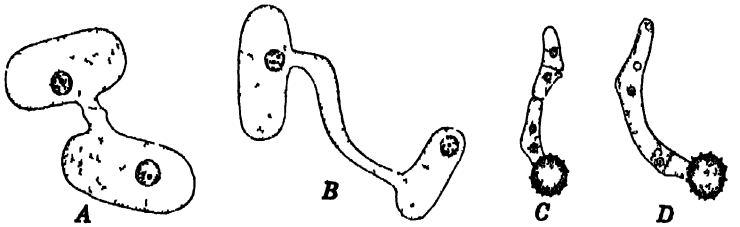


FIG. 262.—*A B*, conjugation of basidiospores of *Ustilago anthearum* Wint. *C-D*, conjugation between cells of basidium of *Ustilago Carbo* Tul (*A B, after Harper*, 1899, *C-D, after Rawitscher*, 1912)

In contrast with Phycomycetae and Ascomycetae, there is never a development of sex organs on mycelia of Basidiomycetae. Despite the lack of sex organs, the life cycle of a basidiomycete involves a change from a condition where the cells are uninucleate (the *haplophase*) to one where they are binucleate (the *diplophase*). The diplophasic condition terminates during basidial development, and the basidiospores represent a return to a haplophasic condition. On the basis of chromosome number, cells of the haplophase are gametophytic, and those of the diplophase are sporophytic. Gametophytic and sporophytic portions of the life cycle may be segregated in separate mycelia or combined in the same mycelium. In the latter case, the first-developed portion of a mycelium has uninucleate cells, and the later-developed portion has binucleate ones. Diplophasic mycelia or portions of a mycelium generally, although not always, have the "clamp connections" described on page 468.

Formation and Development of the Diplophase. The diplophase usually originates through an establishment of a tubular connection between two uninucleate cells and a migration of two nuclei and some of the cytoplasm into the tube The cytoplasm from the two protoplasts becomes intermingled, but there is no fusion of the two nuclei. Certain smuts have this conjugation (Fig 262*C–D*) at the earliest possible stage, that is, between cells of a four-celled basidium.[1] Certain other smuts may have a conjugation of basidiospores (Fig 262*A–B*) or of conidia produced by them [2] In most basidiomycetes other than smuts, conjugation takes place after a basidiospore (or a conidium formed by it) has developed into a haplophasic mycelium. Conjugation in hymenomy-

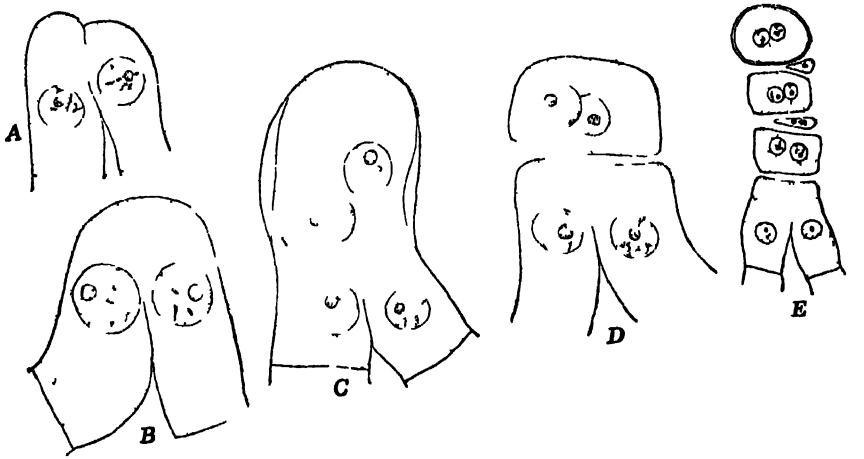


FIG 263 *Phragmidium speciosum* Fries *A D*, stages in conjugation of hyphae to form binucleate aecidiospores *E*, a chain of aecidiospores (*After Christman*, 1905)

cetes and gasteromycetes is generally between vegetative cells of mycelia with uninucleate cells Some of these fungi have conjugation between cells borne on the same mycelium. In a much larger number of cases the mycelia are heterothallic, and conjugation takes place only when two mycelia grow intermingled with each other (Fig 266*A*). Rusts may have a delay in establishment of the binucleate condition until after a haplophase mycelium has produced spores. This may be effected (Fig. 263) by two mycelial cells fusing to form a binucleate spore (aecidiospore),[3] or it may result from fusion of a uninucleate spore with a vegetative cell of the haplophase mycelium.[4]

The binucleate cell formed by conjugation always has a synchronous division of the two nuclei. This is followed by a cell division that dis-

[1] Harper, 1899; Lutman, 1910; Rawitscher, 1912.
[2] Harper, 1899; Lutman, 1910. [3] Christman, 1905; Blackman, 1904.
[4] Andrus, 1931; Allen, 1933.

tributes one pair of daughter nuclei to each of the two daughter cells. In the case of heterothallic species the two nuclei in each cell are of different genetic composition. Division of binucleate cells of the rusts (Uredinales) is simple and by means of a transverse wall formed between the two pairs of daughter nuclei.[1]

One or more species of all orders but the Uredinales have been shown to form "clamp connections" during division of binucleate cells. Here, cell division is usually restricted to terminal cells of hyphal branches. In typical cases a cell about to divide puts forth a short, lateral, arcuate outgrowth that projects downward toward the base of the cell. One nucleus migrates into the outgrowth, the other remains in the cell,[2] after which the two nuclei divide simultaneously (Fig. 264*B–C*). Daughter

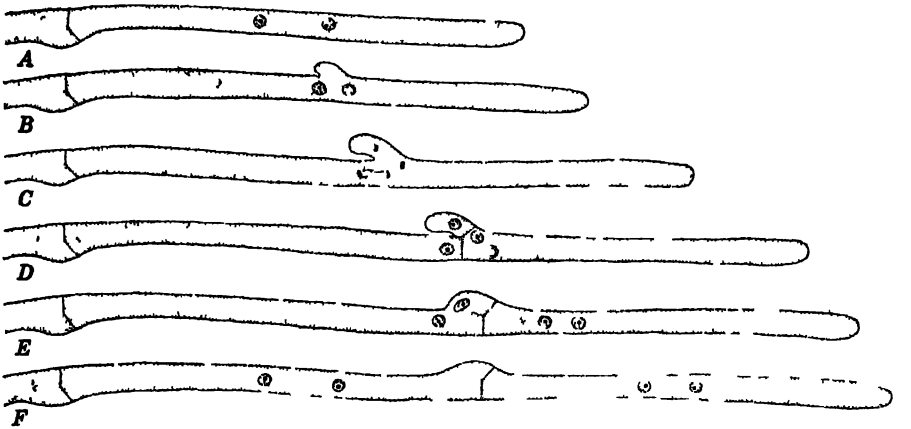


FIG. 264.—Diagram showing the successive stages in formation of a clamp connection in a hypha of *Corticium varians* Kniep. (*Based upon Kniep*, 1915.)

nuclei of that within the cell come to lie some distance apart, one above and the other below the level of the outgrowth. One daughter nucleus of that within the outgrowth remains within the outgrowth; the other lies within the cell. Two transverse septa are now formed, one across the base of the outgrowth, the other across the cell and just below the level of the outgrowth (Fig. 264*D*). The outgrowth is now a uninucleate *clamp cell*. The upper daughter cell formed by transverse division of the original cell is binucleate, the lower daughter cell is uninucleate. Later on the lower cell becomes binucleate by fusing with the clamp cell (Fig. 264*E–F*). With repeated division in this manner, there is a development of a many-celled mycelium whose diplophasic nature is recognizable on account of the numerous clamps.

Spore Formation by the Diplophase. According to the particular genus, there may or may not be a formation of spores that reduplicate

[1] Poirault and Raciborski, 1895; Sappin-Trouffy, 1896.

[2] Bensaude, 1918; Kniep, 1915, 1917.

the diplophase mycelium. Such spores are relatively uncommon among the hymenomycetes and gasteromycetes, but they are generally present in the rusts. Reduplicating spores of the diplophase may be conidia, chlamydospores, or such special types as the uredospores of rusts. All of these various spores are binucleate, and, when they germinate, they give rise to a mycelium with binucleate cells. Binucleate cells of the diplophase may also produce uninucleate spores.[1] A binucleate cell may send out a lateral outgrowth into which a single nucleus migrates. This is followed by an endogenous formation of a chain of uninucleate spores at the apex of the outgrowth. These spores are usually called oïdia, but they are really aplanospores. In rare cases there may be a formation of these spores at the apex of a clamp cell (Fig. 266*B–C*).

The Basidium. Mature diplophasic mycelia of all basidiomycetes produce basidia that bear basidiospores. With the production of basidiospores there is a return to the haplophasic condition. Basidia are formed in two ways. In the smuts and rusts (the *Hemibasidii*) there is a formation of a special spore that germinates to form the basidium. All other basidiomycetes (the *Eubasidii*) have a direct development of basidia from terminal cells of certain hyphae.

The Eubasidii generally have the basidia in a palisade-like layer known as the *hymenium*. The young basidium is always binucleate, and it may[2] or may not have evident clamp connections at its base (Fig. 265*A–D*). As the basidium increases in size, there is a fusion of the two nuclei (Fig. 265*E*). The fusion nucleus divides soon after it is formed, and, in all cases where the division has been studied, it has been shown to be meiotic. Practically all Eubasidii have the fusion nucleus forming four daughter nuclei (Fig. 265*F–G*), but there are a few cases[3] where it divides into eight. Two orders of the Eubasidii (Agaricales and Lycoperdales) have a homogeneous basidium in which there is no differentiation into an early- and a late-developed portion. These basidia produce slender projections (*sterigmata*) at the distal end. Four-nucleate basidia develop two or four sterigmata; eight-nucleate basidia may produce eight of them. Each sterigma increases in size at the upper end, and a nucleus from the basidium migrates into the enlarging portion. A cross wall is eventually formed at the base of the enlargement, and the cell thus cut off is a basidiospore (Fig. 265*H–I*). The remaining three orders of Eubasidii have the basidia differentiated into a lower first-formed portion (the *hypobasidium*)[4] and an upper later-formed portion (the *epibasidium*). Sterigmata are always developed on the epibasidial portion of these basidia. Basidia with a differentiation into epi- and hypobasidia may be unseptate (Fig. 278*B*) or septate. The septation

[1] Brodie, 1936. [2] Kniep, 1916.
[3] Maire, 1902; Juel, 1916. [4] Neuhoff, 1924.

may be in the hypobasidial portion and vertical (Fig. 280*A*) or in the epibasidial portion and transverse (Fig. 282). Sterigmata are produced terminally on vertically divided basidia and laterally on transversely divided ones.

Basidium-producing spores of Hemibasidii are always binucleate and generally thick-walled. With a few exceptions[1] there is a fusion of the two nuclei and a meiotic division of the fusion nuclei into four (rarely eight) daughter nuclei. This may take place before or after the spore has germinated to form the basidium. A large majority of the Hemibasidii have the spore sending out a short hypha-like epibasidium that

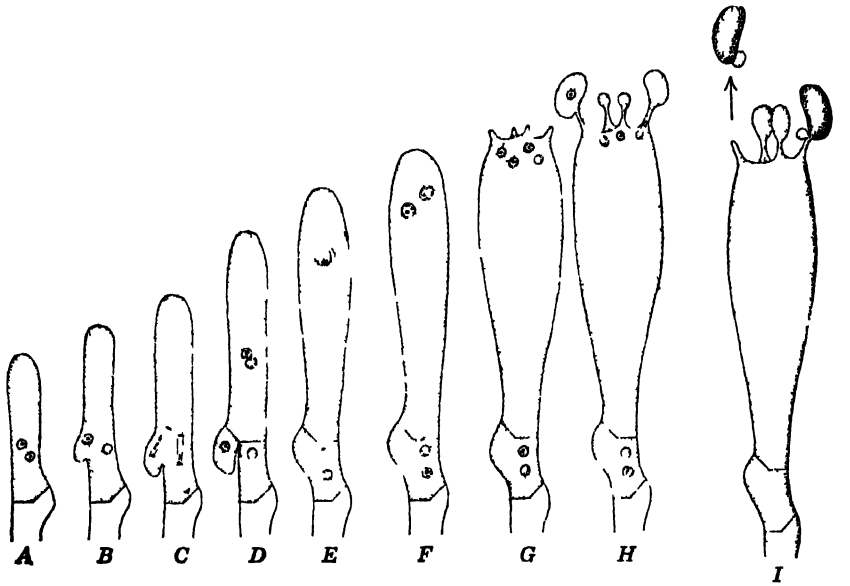


FIG. 265.—Diagram showing successive stages in development of a basidium. (*A H, based upon Knop*, 1928, *I, based upon Buller*, 1922)

becomes transversely divided into four cells, each of which bears one or more basidiospores. Formerly, and before its nature was understood, the epibasidium was called a *promycelium*, and the spores borne upon it were called conidia. In a few Hemibasidii the epibasidium is not transversely septate and the basidiospores are borne terminally.

The Basidiospore. Hymenomycetes, smuts, and rusts have an explosive abscission of a basidiospore from the basidium; one that hurls the spore 0.1 to 1.0 mm.[2] A developing basidiospore always forms a small lateral outgrowth (the *hilum*) near the region of juncture with the sterigma. A minute or so before spore abscission, a small droplet of liquid appears upon the hilum. The droplet grows to about a fifth the size of the spore and then both spore and droplet suddenly

[1] Dodge and Gaiser, 1926. [2] Buller, 1909, 1924.

shoot off from the sterigma (Fig. 265*I*). The mechanism of this abrupt abscission is unknown. Basidiospores on a four-spored basidium are discharged in a regular succession and not simultaneously. The interval between discharge of the first and second spore may be a minute or more; that between discharge of the second and third, or the third and fourth, spores may be somewhat longer.[1] There is also a successive ripening of basidia on hymenia of hymenomycetes. Thus, the period of spore

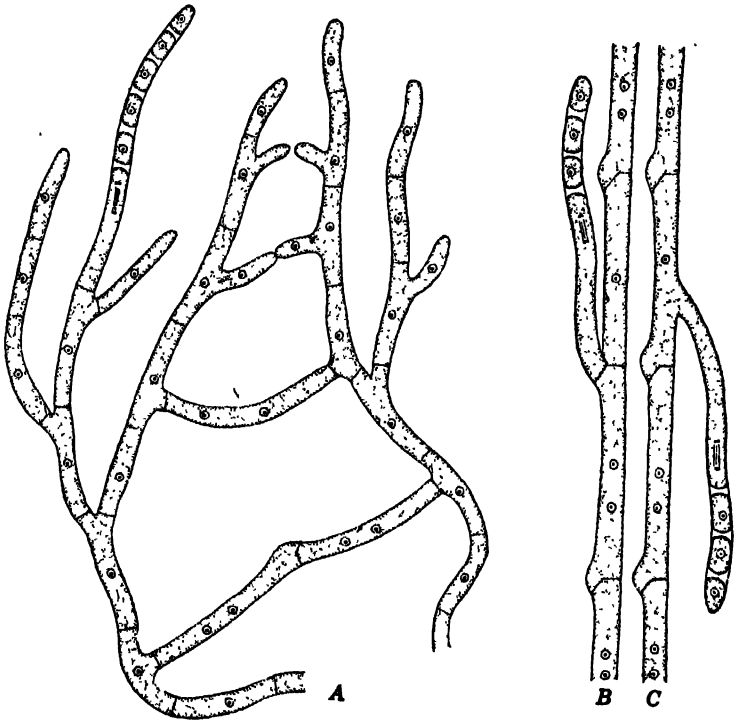


FIG. 266.—*A*, diagram showing formation of diplophasic cells by the conjugation of haplophase mycelia. *B*, diagram showing the formation of haplophase oïdia (aplanospores) by a diplophase mycelium. (*Based upon Brodie*, 1936.)

discharge continues for some time, and, according to the particular species, this may last for hours, days, or even weeks. The number of spores discharged is tremendous, and it has been estimated[2] that large fruiting bodies of certain hymenomycetes shed spores at the rate of a million a minute for 50 hours or more.

The Haplophase. Basidiospores, or the cells of a four-celled basidium, are the first cell generation of the haplophase. As already noted, these may immediately conjugate to form the diplophase. Generally, however, a basidiospore gives rise to a many-celled haplophasic mycelium. The first-formed portion of such a mycelium may be multinucleate,[3] but

[1] Buller, 1924. [2] Buller, 1909. [3] Levine, 1913; Bensaude, 1918.

this soon forms transverse septa that divide into uninucleate cells. Development of a haplophase mycelium may cease with a precocious conjugation,[1] or mycelial development may be quite extensive before conjugation takes place (Fig. 266*A*). In many heterothallic species the mycelium is capable of unlimited growth in case it does not come in contact with a mycelium of the opposite sex. A production of the diplophase from the haplophase is not obligatory in the life cycle of all basidiomycetes since there may be a reproduction by spores that reduplicate the haplophase. Sometimes these spores are conidial in nature; more often they are the type of aplanospores usually called oïdia (Fig. 266*A*).

Origin of the Basidiomycetes. At one time opinion was divided as to whether the basidiomycetae were derived from the Phycomycetae or

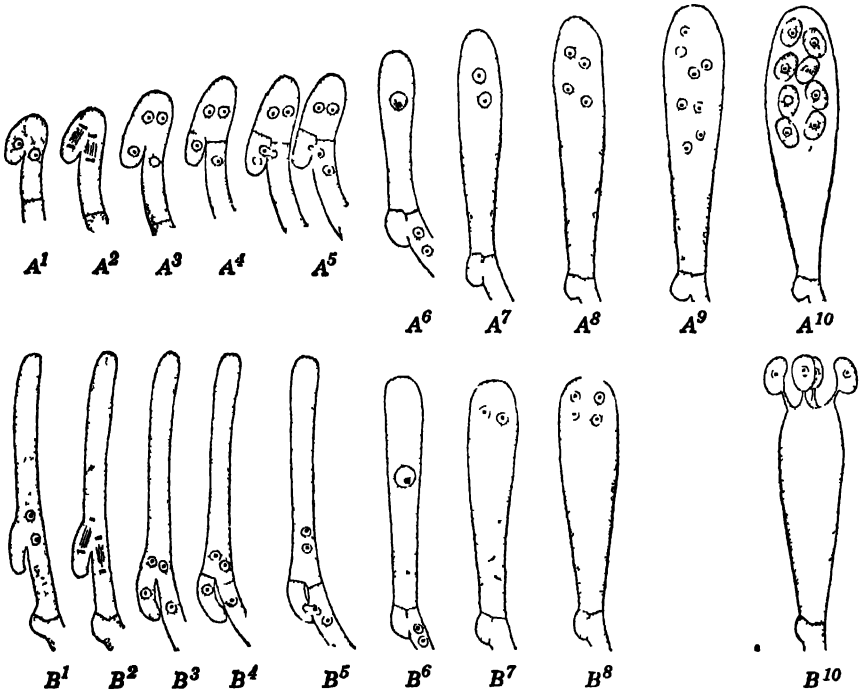


FIG. 267.—Diagram showing similarities in development of an ascus (A^1–A^{10}) and a basidium (B^1–B^{10}). Homologous stages in the two lie vertical to each other. (*Modified from Gäumann and Dodge*, 1928.)

from the Ascomycetae. Practically every mycologist discussing the question during the past two decades argues for a phylogenetic relationship between the ascomycetes and basidiomycetes. The major factor inducing this swing to the ascomycetan hypothesis was the suggestion[2] that basidiomycetean hyphae with clamp connections are homologous

[1] Bensaude, 1918. [2] Kniep, 1915.

with ascogenous hyphae and that there are homologies in early development of asci and basidia (Fig. 267). According to this interpretation[1] the apparently terminal binucleate cell developing into a basidium is really a penultimate cell that lies posterior to a terminal uninucleate cell. Its two nuclei, similar to those in the homologous cell of an ascogenous hypha, unite with each other to form a fusion nucleus that divides meiotically. Thus, the only fundamental change in evolution of an ascus into a basidium has been a change from an endogenous to an exogenous method of spore formation. If the Basidiomycetae have arisen from the Ascomycetae, it is obvious that they must have come from the Euascomycetae rather than the Protoascomycetae. However, nobody has hazarded a guess as to which particular Euascomycetae are the ancestral forms.

Evolution within the Basidiomycetes. There is a general agreement that the tremelloid basidiomycetes (Auriculariales and Tremellales) bridge the gap between the hymenomycetes and the smuts and rusts. On the other hand, there is marked disagreement as to how the evolutionary series should be read. According to one interpretation[2] the evolutionary sequence has been from the smuts and rusts to the tremelloid forms, and from them to the hymenomycetes and gasteromycetes. Another interpretation[3] holds that evolution has been in the reverse direction and that the most primitive of the basidiomycetes are to be found among the hymenomycetes. The relative merit of these two diametrically opposed views rests upon the nature of the basidium. If, as appears to be the case, it is a modified ascus, it follows that Basidiomycetae with an unseptate basidium (hymenomycetes and gasteromycetes) are more primitive than those with a septate one.

Classification of Basidiomycetes. Basidia develop in the two ways that have been described (page 470). This is a character of fundamental importance and the one of greatest significance in dividing the Basidiomycetae into the following two subclasses:

Eubasidii in which there is a direct development of a basidium from a vegetative cell.

Hemibasidii in which the mycelium forms a spore that germinates to form the basidium.

SUBCLASS 1. EUBASIDII

All of the Eubasidii have a direct development of basidia from vegetative cells of the diplophase mycelium. In almost all cases the diplophase mycelium grows into a macroscopic fruiting body of definite form in which the basidia are in a continuous or a discontinuous layer, the *hymenium*. Hymenia of mature fruiting bodies may be freely exposed or permanently

[1] Kniep, 1915. [2] Dietel, 1928; Gwynne-Vaughan and Barnes, 1927.
[3] Kniep, 1928; Gäumann and Dodge, 1928.

surrounded by sterile tissue. The subclass contains some 335 genera and 17,000 species. Less than 10 per cent of the genera are parasitic or have parasitic species; all others are saprophytic.

There is no universal agreement as to the number of orders that should be recognized among the Eubasidii. However, all systems of classification take into account both the basidia and the structure of the fruiting body upon which they are borne. On the basis of these two characters the Eubasidii may be divided into five orders.

ORDER 1. AGARICALES (HYMENOMYCETAE)

The Agaricales have basidia that are freely exposed from the beginning or become exposed before they produce spores. The basidia are unseptate, are club-shaped, and lie in a continuous or discontinuous layer one cell in thickness. They generally bear two or four basidiospores, but they may bear up to eight of them. A few genera have an amorphous thallus, but most of them have a fruiting body of definite macroscopic form. The order includes some 175 genera and 16,000 species. All but a very few of the species are saprophytic.

The Agaricales are divided into seven families[1] differing from one another in organization of the fertile layer. In two families there is no fruiting body. Two of the five families with a definite fruiting body have a smooth hymenial surface that is restricted to one surface of the fruiting body or, as in the coral fungi, covers all sides of it. The three families in which the hymenium is not smooth may have it spread over radiate plates as in the gill fungi (mushrooms), spread over conical protuberances as in the spine fungi, or lining small pores as in the bracket fungi.

Exobasidium is one of the few parasitic genera of the order. It is also one of the genera in which there is not a definite fruiting body. It is uncertain whether this simple plant body should be interpreted as primitive or as one in which there has been a reduction from a definitely organized fruiting body. The genus includes about 20 species. One of them causes a gall disease of cranberries and huckleberries; another causes a leaf blister of tea. *E. Vaccinii* (Fckl.) Wor., the species parasitic on cranberries, infects both leaves and twigs. The host cells in an infected area divide repeatedly and mature into a solid parenchymatous tissue of uniform texture.[2] An infected area is externally recognizable both on account of its gall-like appearance and on account of its red color. The mycelium of *E. Vaccinii* is intercellular and composed of many very narrow hyphae. Most of them lie between subepidermal cells of the host but some penetrate deeper. A mycelium may produce conidia.

[1] Killermann, 1928. [2] Pelluet, 1928; Eftimiu and Kharbush, 1927.

They may be borne on hyphae that project beyond the epidermis of the host or upon hyphae that lie intermingled with the basidia.[1]

Basidia develop on erect unicellular hyphal branches growing up between and extending beyond the epidermal cells of the host (Fig. 268). The basidia become club-shaped and several times broader than a hyphal branch. A young basidium is binucleate. During further development there is the usual fusion of the two nuclei and a subsequent division of the fusion nucleus.[2] The fact that a basidium may produce up to seven basidiospores shows that the fusion nucleus may form eight daughter nuclei. Basidiospores are developed upon terminal sterigmata in the usual manner [1] Unlike most other Agaricales, the basidiospores are elongate, and they may form one or two transverse septa before or

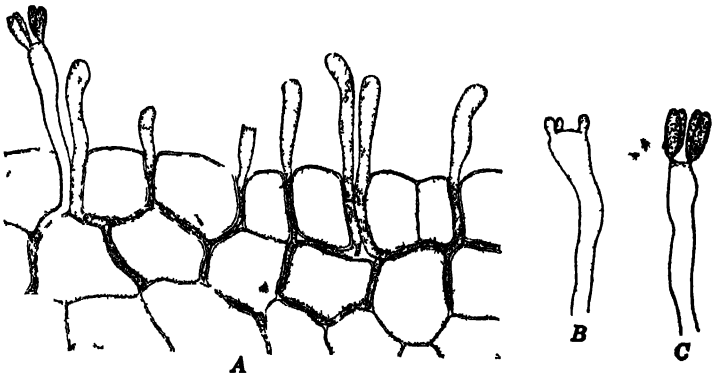


FIG 268 —*Exobasidium* sp *A*, fruiting mycelium and host cells *B–C*, stages in development of a basidium (*A*, × 430, *B–C*, × 650)

after abscission. Germinating two- or three-celled basidiospores may bud off a conidium from each cell, and each conidium may bud off further conidia in a yeast-like manner

Psalliota campestris (L) Fries [*Agaricus campestris* L], the common "field mushroom," is representative of those Agaricales in which the fruiting body is highly developed and has the basidia borne on gills (Fig. 269). It is the one species that is cultivated for the market. *P. campestris* has a subterranean mycelium in which the hyphal branches radiate from a common center and produce fruiting bodies toward the periphery. A fruiting body (the mushroom) begins to develop underground, but it eventually grows up through the soil to a height of 5 to 9 cm. Subterranean mycelia of *P. campestris* are perennial and increase in diameter from year to year. Centrifugal extension of the mycelium is accompanied by a death of old hyphae in the central portion. Thus, when growth conditions are favorable in lawns and pastures, the fruiting bodies appearing above ground lie in a ring Such circles of mushrooms

[1] Richards, 1896. [2] Ritzimu and Kharbush, 1928; Maire, 1902.

are often called "fairy rings," a name based on the ancient belief that these circular growths marked the path of dancing fairies. Perfect fairy rings of *Psalliota* are usually less than 5 meters in diameter, but perfect rings more than 50 meters in diameter have been found.[1] Imperfect rings of certain other Agaricales may attain a diameter of more than 400 meters.

One of the strains of *P. campestris* cultivated by mushroom growers is homothallic.[2] The basidiospore of the cultivated mushroom is multinucleate.[3] When it germinates, it sends forth a hypha that soon becomes branched and transversely septate.[4] It is very probable that the cells are multinucleate, but this has not been demonstrated. Conjugation takes place early in mycelial development,[4] and the union may be between

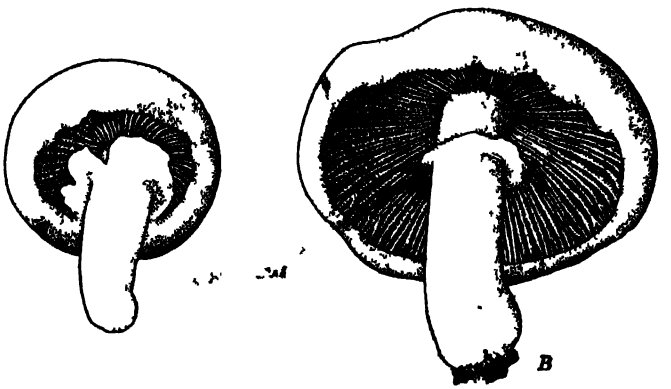


FIG. 269.—*Psalliota campestris* (L.) Fries. *A*, nearly mature fruiting body. *B*, mature fruiting body. ($\times \frac{2}{3}$)

cells that lie side by side or end to end. Later-developed hyphae are atypical for Eubasidii in that their cells are multinucleate instead of binucleate.[5] This coenocytic nature of the cells is the probable reason for the failure[6] to find clamp connections in the cultivated mushroom. Hyphae of a centrifugally developing mycelium may lie free from one another or lie in small rope-like strands (*rhizomorphs*). Certain of the hyphae in a rhizomorph are of much larger diameter than others, and it has been shown[4] that the larger hyphae are produced by a lateral fusion of smaller ones.

Fruiting bodies are formed in the rhizomorphic portion of a mycelium. Many primordia of fruiting bodies are differentiated upon the rhizomorphs, but only a small percentage of them develop to maturity.[7] A young primordium is a broadly ovoid solid mass of interwoven hyphae in which those at the periphery are less densely compacted than those at

[1] Shantz and Piemeisel, 1917. [2] Lambert, 1929. [3] Sass, 1929.
[4] Hein, 1930. [5] Hirmer, 1920; Sass, 1929.
[6] Hein, 1930; Hirmer, 1920; Sass, 1929. [7] Hein, 1930*A*.

the interior. At the time when a young mushroom is about 1 mm. in height, there is a differentiation of a transverse internal ring of parallel vertical hyphae—the *hymenial primordium* (Fig. 270*A–B*). The portion of the fruiting body above the hymenial primordium eventually develops into the cap (*pileus*) of the mature mushroom; that below it develops into the stalk (*stipe*) and base. The lower face of the hymenial primordium soon pulls away from the immediately underlying hyphae to form a transverse internal annular cavity, the *prelamellar chamber*.[1] Then the lower face of the hymenial primordium becomes concave and differ-

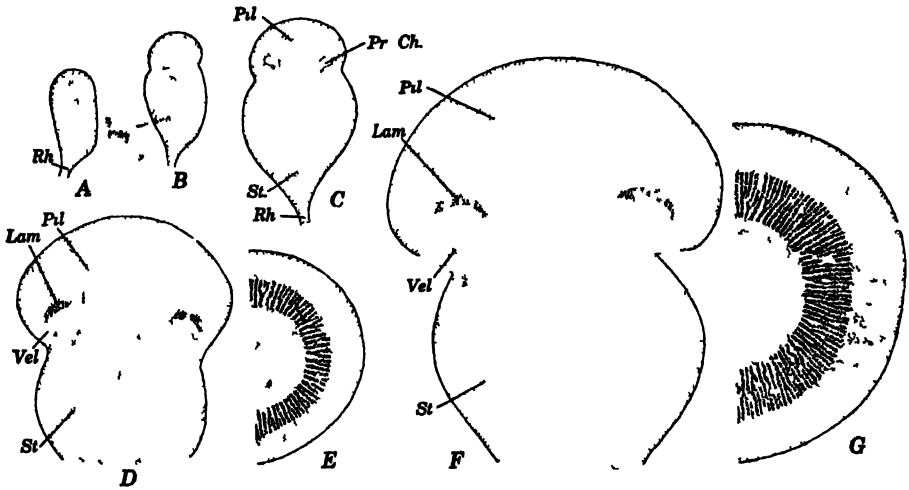
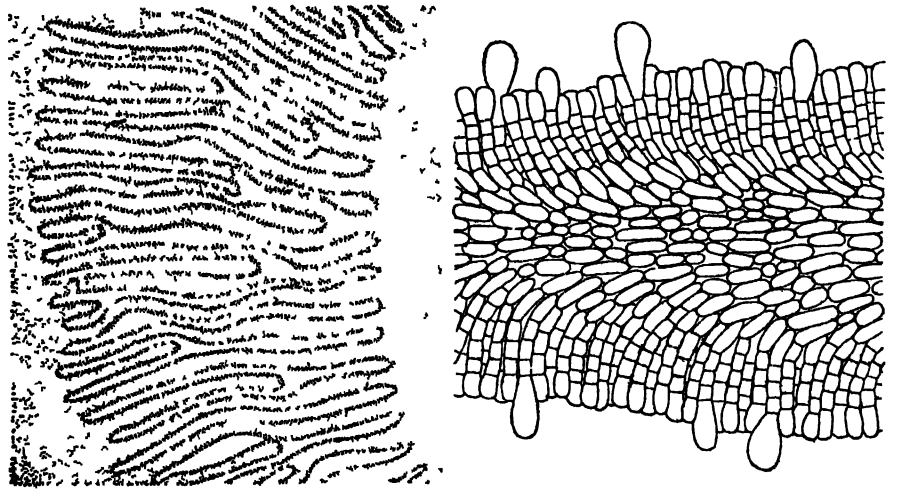


FIG 270 —*Psalliota campestris* (L.) Fries Stages in development of fruiting bodies *A–B*, before appearance of prelamellar chamber *C*, after appearance of prelamellar chamber *D–G* vertical and transverse section of two fruiting bodies with developing lamellae (×3) (*Lam*, lamellae *Pil* pileus, *Pr Ch*, prelamellar chamber, *Rh* rhizomorph, *St*, stipe, *Vel*, velum)

entiated into many alternate radial bands of slow- and fast-dividing cells Each radial band of fast-dividing cells is a gill primordium, and it soon develops into a young gill (*lamella*) that projects downward into the prelamellar chamber (Fig. 270*C*). The diameter of a pileus increases greatly after the lamellae begin to develop. As a result, there is a constant broadening of the outer portion of the radial interspaces between the lamellae. Additional gill primordia develop in the broadening interspace between two primary gills, but these secondary gills never have a radial length equal to that of the primary ones The formation of secondary gills may be due to a Y-like splitting of a primary gill (Fig. 271*A*), or to a downward growth of tissue from the roof of the prelamellar cavity. A young fruiting body is about 1 cm. tall and with a breadth slightly less than the height at the time the secondary gills

[1] Hein, 1930*A*.

begin to appear. Further growth may be very rapid since it is largely an elongation of cells of this "button stage." Thus the sudden appearance of mushrooms in a meadow after a rain is due to cellular enlargement rather than to a formation of new cells. Mushrooms at the "button stage" of development have the edge of the pileus joined to the stipe by a thin sheet of tissue, the veil or *velum*. Enlargement of the pileus ruptures the velum, but a ring-like remnant of it, the *annulus*, remains attached to the upper part of the stipe (Fig. 269*B*). An expanded pileus has the lamellae on its lower face, and they radiate from the stipe to the



A *B*

FIG. 271.—*Psalliota campestris* (L.) Fries *A*, enlarged portion of lamellar region of Fig. 270*G*. *B*, semidiagrammatic transverse section of a young lamella (*A*, × 21, *B*, × 650.)

pileal margin. Mature pilei of *P. campestris* bear between 300 and 600 gills.[1]

As seen in transverse section (Fig. 271*B*), a young lamella consists of three tissues: a superficial palisade-like layer of basidia; beneath this a subhymenial tissue of isodiametric cells; and internal to this a region of elongate cells, the *trama*, so oriented that their long axes lie at right angles to the palisade layer. The apparently parenchymatous subhymenial layer is really a series of vertical hyphal branches from the trama and one in which the terminal cell of each branch is a basidium. The tramal and innermost subhymenial cells are multinucleate; the outermost subhymenial cells and the basidia are binucleate.[2] The basidial layer is frequently described as consisting of fertile cells (basidia) and sterile cells (paraphyses). In reality the so-called paraphyses are immature basidia that have not yet formed spores.[1]

[1] Buller, 1922. [2] Colson, 1935; Hirmer, 1920; Sass, 1929, 1936.

Basidial development (Fig. 272) is in the manner typical of the Agaricales. A young basidium is binucleate, and the two nuclei unite with each other to form a fusion nucleus that divides meiotically into four daughter nuclei.[1] Sterigmata appear after nuclear division is completed; two on basidia of the cultivated form of *P. campestris* and two or four on the wild forms. The form with two sterigmata has two nuclei migrating into each sterigma[2] and then spore formation in the usual manner. The nuclei in basidiospores from both two- and four-spored basidia undergo at least one division before the spore is discharged from the basidium.

Basidiospore abscission from both bisporous and quadrisporous basidia is immediately preceded by the accumulation of a droplet of

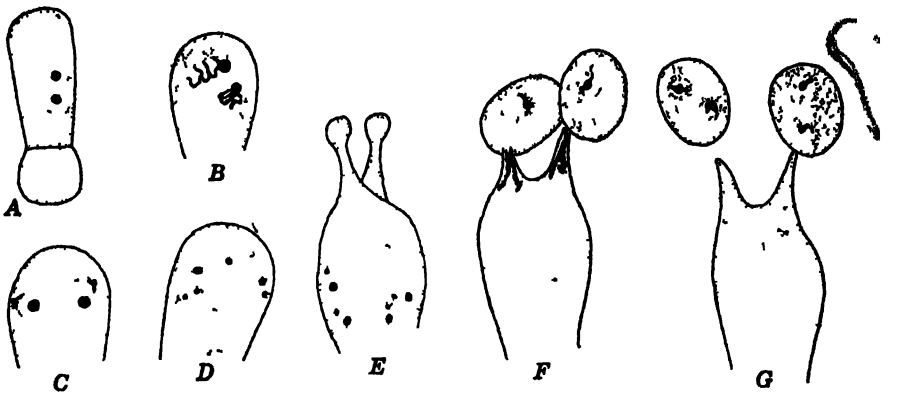


FIG. 272.—Stages in development of basidia of *Psalliota campestris* (L.) Fries (*After Colson*, 1935) (× 2,250)

liquid on the hilum.[3] The forcible ejection of the basidiospore is so nicely balanced that the spore is hurled beyond the hymenial surface but not across the interlamellar cavity and against the next lamella. After being shot out horizontally into the interlamellar chamber, the spore falls vertically downward. The trajectory of a basidiospore is unique among those of horizontally discharged projectiles. The trajectories of other projectiles are paraboloid curves; that of a basidiospore makes a right-angled downward turn.[4] Spore discharge from lamellae of *Psalliota* is continuous and may last more than five days. It has been estimated[4] that a pileus of average size discharges more than ten billion spores.

ORDER 2. LYCOPERDALES (GASTEROMYCETAE)

The Lycoperdales have unseptate basidia which produce basidiospores at the distal end. The basidia may remain permanently enclosed within

[1] Sass, 1929; Maire, 1902. [2] Colson, 1935; Sass, 1929.
[3] Buller, 1922. [4] Buller, 1909.

sterile tissues of a fruiting body, or the external sterile tissue may rupture and expose the basidia after they have formed spores. The order includes the puffballs, the false truffles, the earth stars, the bird's-nest fungi, and the stinkhorn fungi. There are about 120 genera and some 1,100 species, all saprophytic. These are divided into eleven families.

All members of the order are saprophytic. The mycelia of many species grows in the soil, but those of certain species grow in decaying wood. Terrestrial species may develop their fruiting bodies above or below the surface of the soil. Basidiospores of some aerial Lycoperdales are dispersed by wind; those of other aerial, and of all subterranean, fruiting bodies are dispersed by animals that feed upon them, the spores passing undigested through the alimentary tract of the animal. These animals include various insects, slugs, and rodents Animals feeding upon gasteromycetes are generally attracted to them by the strong odor emitted by the fruiting body.

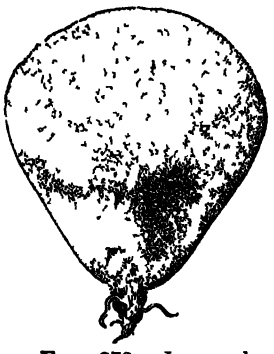


FIG. 273 —*Lycoperdon pyriforme* Schaeffer. (Natural size)

The complete life history is known for only a few species. In the cases where this has been followed from the beginning, it has been shown that the basidiospore may germinate into a haplophasic mycelium with uninucleate cells,[1] or into a mycelium that is diplophasic from the beginning.[2] Hyphae of fruiting bodies of many species are known to be composed of binucleate cells, and in many cases there are evident clamp connections. In all cytologically investigated cases basidial development includes a fusion of two nuclei and a reductional division of the fusion nucleus.[3]

All of the species of *Lycoperdon* are puffballs. The fruiting body (the "puffball") is globose to pyriform accordingly as the sterile basal portion is or is not elongated into a definite stalk (Fig. 273). Fruiting bodies of *Lycoperdon* are rarely more than 8 cm. in diameter but those of other puffballs may be much larger A species of a genus closely related to *Lycoperdon* has a fruiting body that frequently attains a diameter of 50 cm. In one exceptional case[4] a specimen 160 cm. in diameter was found.

Basidiospores of *Lycoperdon* usually germinate only after they have been alternately moistened and dried for several times.[5] When the spore germinates (Fig. 274*E*), it gives rise to a haplophasic mycelium with short uninucleate cells.[5] Older portions of a mycelium bearing fruiting

[1] Swartz, 1929; Lorenz, 1933. [2] Pillay, 1923; Walker, 1927.
[3] Lorenz, 1933; Walker, 1927; Lander, 1933*A*, 1934; Maire, 1902; Fries, 1911.
[4] Bessey, C. E., 1884. [5] Swartz, 1929.

bodies are composed of binucleate cells,[1] but the method of origin of this diplophasic condition is unknown. Hyphae of the diplophase lie in a branching system of rhizomorphs. Rhizomorphs of *Lycoperdon* are more complex than those of *Psalliota* and are composed of three concentric tissues:[2] an outer cortex of loose hyphae, a subcortical layer of compact hyphae, and a central core of parallel hyphae.

Primordia of fruiting bodies arise either laterally or terminally on a rhizomorph and by an outgrowth of hyphae from the central core.[2] Young primordia about 0.5 mm. in diameter are homogeneous in structure and composed of tightly interwoven hyphae. Those slightly larger show a beginning of differentiation into what eventually becomes the outer sterile region (*peridium*) and the inner fertile region (*gleba*). Differentiation of the peridium begins with an outgrowth of a compact palisade-like layer of hyphae over the entire surface of the primordium. The outer portion of this layer, the *exoperidium*, soon becomes pseudoparenchymatous; the inner portion, the *endoperidium*, remains palisade-like.[3] The exoperidium develops numerous radial cracks as a fruiting body increases in diameter, and eventually most of the exoperidium may flake away. At the time of formation of exo- and endoperidium, the interior region (the embryonic gleba) of a young puffball is a homogeneous mass of interlaced hyphae. Here and there in this tissue are small regions where the hyphae begin to pull away from one another to form cavities containing very loosely interwoven hyphae with many broken ends.[1] Many newly formed hyphal branches grow toward the cavity and they become arranged in a palisade-like layer encircling it (Fig. 274*B*). As the puffball increases in size, there is a continuous formation of new cavities (Fig. 274*A*). The first-developed cavities increase greatly in size and become elongated and irregularly lobed (Fig. 274*C–D*). They eventually develop basidia from the enclosing palisade layer. Later-developed cavities remain small, spherical in shape, and sterile.[4]

Basidia developing from the palisade layer of fertile cavities are short and plump. They have the usual fusion of two nuclei and a reduction division of the fusion nucleus into four daughter nuclei.[5] Four sterigmata and spores are usually formed on a basidium, but sometimes there are only two or three.[6] Basidiospores of *Lycoperdon* are globose and with the spore wall variously ornamented.

A mature puffball has a dry and leathery sterile jacket, the endoperidium, in which there is a small circular opening at the summit. At this time the gleba consists of a powdery mass of spores intermingled with various sterile tissues (hyphae, walls of sterile cavities, and walls of

[1] Lander, 1933. [2] Lander, 1933; Swartz, 1933.
[3] Cunningham, 1926; Lander, 1933. [4] Lander, 1933; Rehsteiner, 1892.
[5] Maire, 1902. [6] Coker and Couch, 1928.

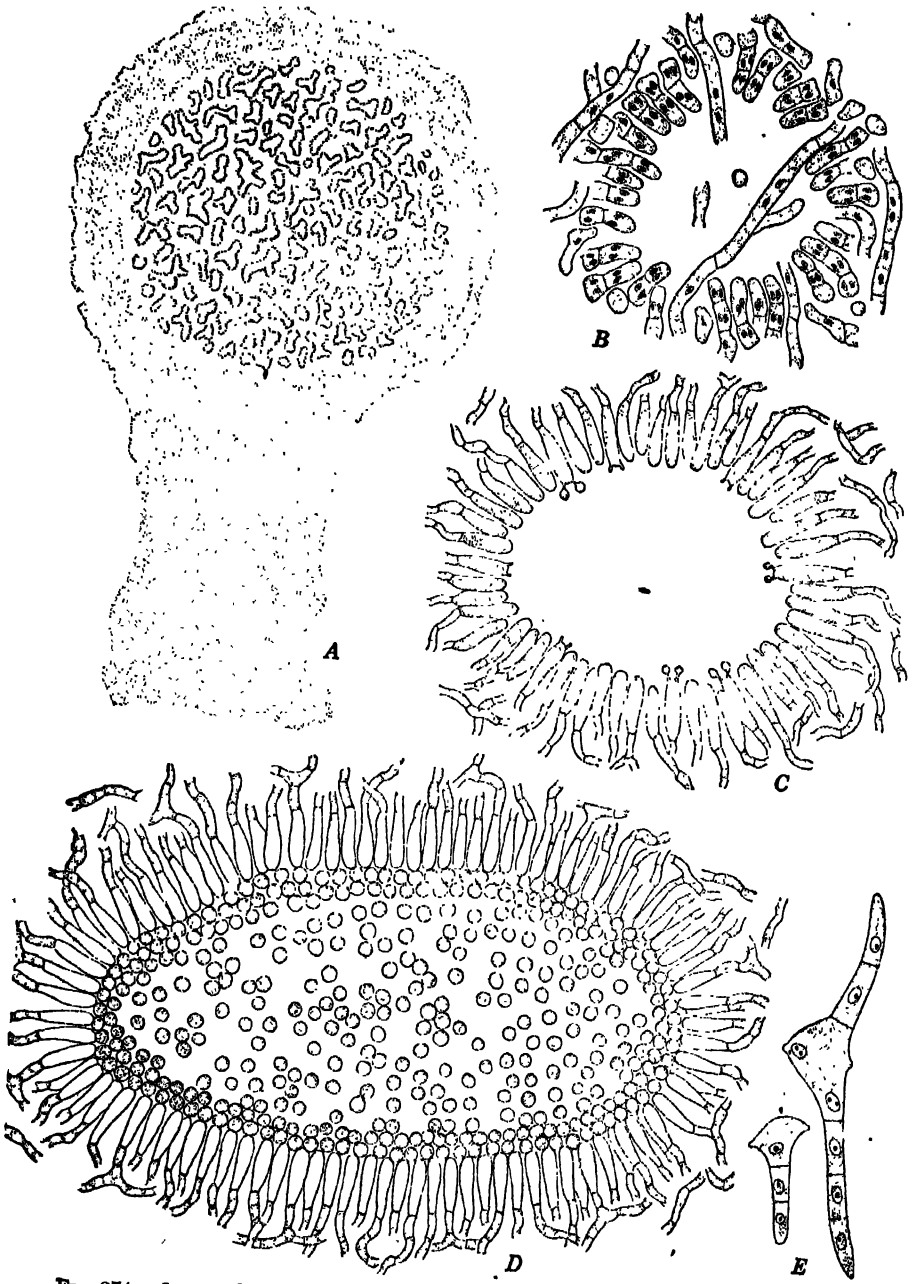


FIG. 274.—*Lycoperdon gemmatum* Batsch. *A*, vertical section of a young fruiting body. *B*, a very young glebal cavity before the formation of basidia. *C*, glebal cavity at the beginning of basidiospore formation. *D*, old glebal cavity. *E*, germination of basidiospores. (*E*, *after Swartz*, 1929.) (*A*, × 21; *B–D*, × 650; *E*, × 1,000.)

fertile cavities) that jointly constitute the *capillitium*. When a ripe puffball is indented by some external force, the peridial wall acts as a bellows that blows out a cloud of spores. In most cases this pressure is due to strong winds, but it may be due to animals touching the puffball.

Ithyphallus (Fig. 275*A*), one of the stinkhorns, is representative of the Lycoperdales in which basidiospores of a mature fruiting body are freely exposed. *Ithyphallus* generally grows in soil containing rotten

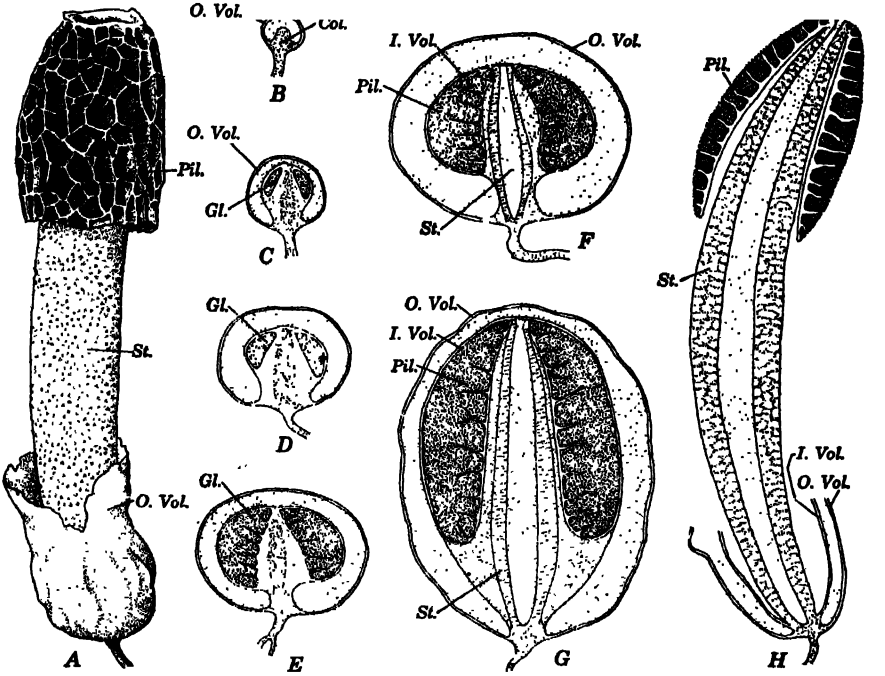


FIG. 275.—*Ithyphallus impudicans* (L.) Fries. *A*, surface view of a mature fruiting body. *B-G*, vertical sections of "eggs" at successive stages of development. *H*, longitudinal section of a mature fruiting body. (× ¾.) (*Col.*, columella; *Gl.*, gleba; *I. Vol.*, inner volva; *O. Vol.*, outer volva; *Pil.*, pileus; *St.*, stipe.)

wood. Habitats of this fungus include old woodpiles, rotting trash piles, and sawdust piles around lumber mills. A mycelium generally bears several fruiting bodies. Anyone who has encountered *I. impudicans* (L.) Fries growing in abundance has cause to remember the incident because of the indescribable stench emanating from the fruiting bodies.

Nothing is known concerning spore germination nor as to whether or not there is a haplophase mycelium of uninucleate cells. The mature mycelium of *I. impudicans* is subterranean and organized into smooth, string-like rhizomorphs. Sometimes a rhizomorph develops into an irregularly shaped sclerotium.[1] A rhizomorph has a compact central core of more or less parallel hyphae surrounded by a cortical sheath of

[1] Overholts, 1925.

loosely interwoven and irregularly branched hyphae. Clamp connections are evident here and there in the cortical sheath.

Primordia of fruiting bodies generally develop at the tips of rhizomorphs, and the diameter of a primordium soon increases to several times that of the rhizomorph. The only evident internal differentiation is an axial strand that is a continuation of the central core of the rhizomorph. As development continues, there is an appearance of a thick, dome-shaped region of very loosely interwoven hyphae that lie toward the distal end and inward from the surface. There is soon a secretion of a dense gelatinous substance that fills all interspaces between the hyphae of this region. By the time a primordium has attained a diameter of 2 mm., the gelatinous region has become a very conspicuous dome which overlies a small *columella* (Fig. 275*B*). The tissue external to the



FIG. 276.—*Ithyphallus impudicans* (L.) Fries. *A*, vertical section of a portion of a young gleba. *B*, basidium. (*A*, × 60, *B*, × 1,300.)

gelatinous region develops into the outer sterile envelope (*outer volva*) that is ruptured as the fruiting body elongates. The portion of the columella immediately next the gelatinous zone develops into a sterile sheath (the *inner volva*) that is also ruptured as the fruiting body elongates (Fig. 275*G–H*). The remainder of the columella develops into the pileus and stipe of the mature fruiting body. The fertile portion of the fruiting body, the gleba, is developed on the external portion of the pileus just within the inner volva (Fig. 275*C–E*). As in *Lycoperdon*,[1] there are numerous fertile cavities within a developing gleba (Fig. 276*A*). The tissues just within the gleba develop into the sterile portion of the pileus, and the innermost tissues of the young columella develop into the hollow

[1] Fischer, 1891, 1893; Atkinson, 1911.

stipe of a mature stinkhorn. The mature pileus and stipe are free from each other except at the apex.

Basidial development has not been followed in detail, but it has been shown[1] that the young basidia are binucleate and that somewhat older ones are uninucleate. Mature basidia are club-shaped and with eight spores at the distal end (Fig. 276*B*). Basidiospores of a nearly mature fruiting body lie in a sticky viscous matrix resulting from disintegration of the basidia and the sterile glebal tissues.

The fruiting bodies remain underground until after the basidiospores are mature. They are ovoid and up to 4.5 by 6 cm. Unopened fruiting bodies are often called "eggs," and they may remain in the unopened "egg" stage for a considerable time (Fig. 275*G*). At any time when conditions are favorable, there is an elongation of the stipe that pushes the pileus through both the inner and outer volva (Fig. 275*A*, *H*). Eggs often open a few hours after they have been removed from the ground, and the stipe pushing through the volvae elongates at a rate of 2 cm. or more an hour. Fully elongated stipes are 7.5 to 15 cm. tall and with a pileus up to 4.5 cm. in length. Insects are the major agency in spore dispersal. The viscous matrix containing the basidiospores is sweetish in taste and is eaten by carrion flies attracted by the strong smell of the fruiting body. Spore dispersal may also be due to rains washing basidiospores from the pileus.

ORDER 3. DACRYOMYCETALES

The Dacryomycetales have basidia in which the distal end of the hypobasidium bears two divergent epibasidia. These Y-shaped basidia are not overlain by sterile tissue at any stage of development. The fruiting bodies are minute, are gelatinous to waxy in texture, and have a definite or indefinite form. The order contains 7 genera and less than 100 species. All genera are saprophytic on dead wood.



FIG. 277.—*Dacryomyces aurantius* (Schw.) Farlow. (Natural size.)

Dacryomyces is a rather widely distributed genus, but its fruiting bodies are apt to be overlooked because they are rarely more than 2 to 3 mm. in diameter. *Dacryomyces* often grows on old boards in gardens. The fruiting bodies are generally yellowish to a deep orange. They are hemispherical to subspherical and with or without a very short stalk (Fig. 277). In dry weather they are greatly shrunken and very difficult to find; after a rain they imbibe water and regain their former size and color.

[1] Maire, 1902.

A basidiospore is uninucleate and unicellular when discharged from a basidium,[1] but it soon becomes transversely, divided into several uninucleate cells, each of which may give rise to a mycelium (Fig. 278*C–E*). Sometimes each cell of a basidiospore buds off several conidia.[2] The mycelium developing from a cell of a basidiospore is haplophasic and with relatively short uninucleate cells (Fig. 278*F*). Hyphae of the

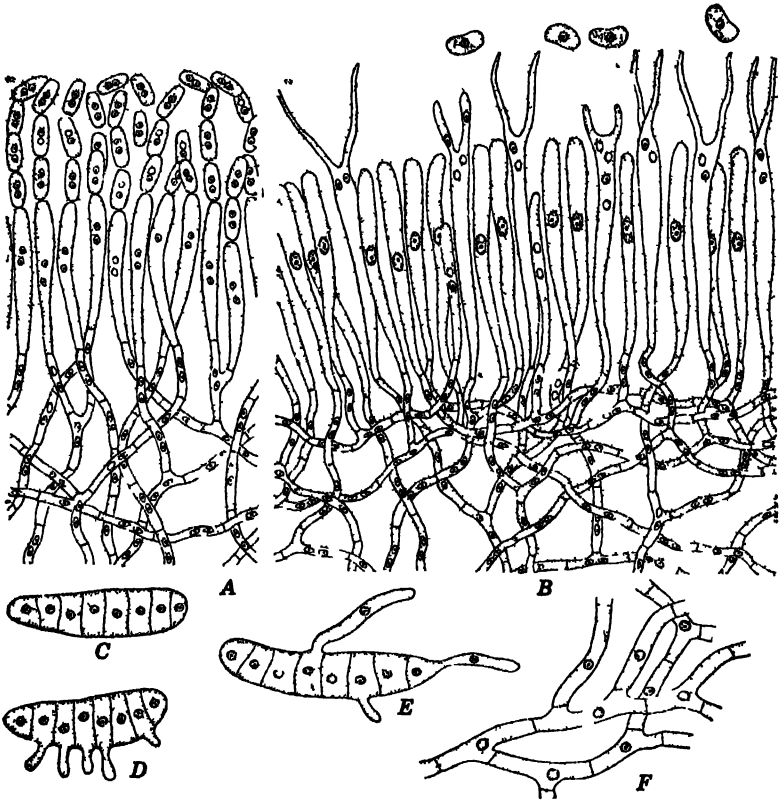


FIG. 278.—*A–B*. *Dacryomyces deliquescens* (Bull.) Duby *A*, diagrammatic vertical section of a portion of a thallus producing oidia *B*, diagrammatic vertical section of a portion of hymenium with basidia at various stages of development *C–F*, *Dacryomyces* sp. *C–E*, germination of spores. *F*, portion of a haplophase mycelium. (*A–B*, × 975; *C–F*, × 1,300.)

fruiting body are composed of binucleate cells, but the stage of development at which there is conjugation to form the diplophase has not been determined.[1] Mycelia growing in artificial culture may produce numerous conidia.[2]

Growth of the fruiting body of *D. deliquescens* (Bull.) Duby is at a very slow rate, and basidia are not developed until the third year.[2] A developing fruiting body of *Dacryomyces* consists of a densely interwoven

[1] Gilbert, 1911, 1921. [2] Brefeld, 1888.

mass of branched diplophasic hyphae in which the hyphal interspaces are filled with a gelatinous substance. Hyphal branches at the surface of a developing fruiting body lie in a palisade-like layer. During the second, and possibly the first, year there is a formation of oïdia at the periphery of the fruiting body. Fruiting bodies of *D. deliquescens* producing oïdia are orange colored; those producing basidia are yellowish.[1] Oïdia (Fig. 278*A*) are developed on relatively stout hyphae that divide transversely into a number of binucleate oïdia, each with a length about double the breadth.[2]

The basidia arise in a palisade-like tissue, often called the hymenium, at the periphery of the fruiting body. The hymenium is often described as consisting of fertile cells (basidia) and sterile ones (paraphyses). However, there is good reason for believing that the so-called paraphyses are immature basidia. A very young basidium is binucleate, and, during its further development, there is a union of the two nuclei and a reductional division of the fusion nucleus into four daughter nuclei (Fig. 278*B*). During these divisions, or shortly afterward, the two divergent projections (epibasidia) grow out from the basidial apex.[3] Each epibasidium develops a small apical sterigma after it has grown through the gelatinous matrix of the fruiting body. A single nucleus migrates into the basidiospore developing on each sterigma. The other two nuclei remain in the hypobasidium[4] or in the two epibasidia.[5] The time between beginning of the spore enlargement at the sterigmatal apex and abscission of the basidiospore is about 50 minutes.[6] There is the usual forcible ejection of a basidiospore shortly after a droplet of liquid has accumulated on the hilum. Basidiospores of *D. deliquescens* are shot 0 5 to 0.65 mm. outward from the sterigmata.[6]

ORDER 4. TREMELLALES

The Tremellales have a basidium in which the first-developed portion (hypobasidium) becomes vertically divided into two, three, or four cells, each of which develops an epibasidium at the distal end. The basidial layer may or may not lie beneath a layer of sterile tissue before basidiospores are formed. The fruiting body is generally gelatinous in texture and more or less indefinite in shape. The order includes about 18 genera and 85 species. Two or three species are parasites, the remainder are saprophytes.

A germinating basidiospore becomes transversely divided into two or more uninucleate cells, each of which may give rise to a mycelium that may produce conidia. Presumably, the mycelium is composed of uninucleate cells, but this has only been definitely established for two

[1] Brefeld, 1888; Tulasne, 1853. [2] Dangeard, 1895.
[3] Juel, 1898; Dangeard, 1895; Gilbert, 1921; Istvánffi, 1895.
[4] Gilbert, 1921. [5] Istvánffi, 1895; Juel, 1898. [6] Buller, 1922.

genera.[1] Hyphae of the fruiting body are generally binucleate and with numerous anastomoses.[2] One species of a genus may have clamp connections; another species of the same genus may lack them.[3]

Tremella is a genus with about 20 species. One of these (*T. myceto-phila* Peck) is parasitic on certain Agaricales; the others grow as saprophytes on decaying wood. The fruiting body of *Tremella* is gelatinous in texture, is more or less rounded, and has the surface variously convoluted (Fig. 279).

The mycelium of *Tremella* ramifies through and absorbs food from the substratum. It consists of branching hyphae with binucleate cells that may or may not have clamp connections.[3] The fruiting body is developed from hyphae that have grown above the substratum. These hyphae are somewhat larger and more intertwined than those in the substratum, and all interspaces between them are filled with gelatinous

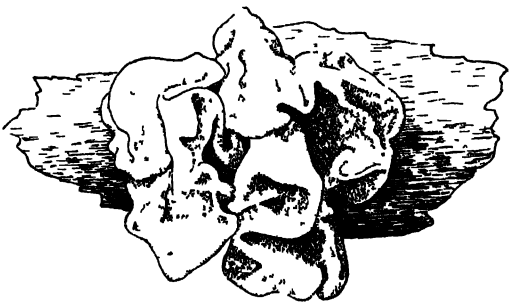


FIG. 279.—*Tremella* sp. (Natural size.)

material. The fruiting body of *T. mesenterica* Retz. may form binucleate oïdia. These are produced in short catenate series from hyphal tips just within the periphery of the gelatinous matrix.[4] The formation of oïdia is coincident with and not, as in *Dacryomyces*, prior to formation of basidiospores. *T. lutescens* Pers. forms conidia that are borne in clusters on short lateral branches.[5]

The entire exposed surface of a fruiting body is fertile. The fertile region consists of a palisade-like layer of narrow branched or unbranched multicellular hyphal tips (paraphyses). Intermingled with them and of approximately the same height are much broader unicellular *cystidia* (Fig. 280*A*). These appear to be modified basidia rather than modified vegetative cells. Their function is unknown. The first indication of basidial development is a dense accumulation of protoplasm in tips of certain hyphae just below the paraphyses and cystidia. The terminal cells of these hyphae become globose (Fig. 280*B–D*), the two nuclei

[1] Gilbert, E. M., 1911; Neuhoff, 1924.
[2] Dangeard, 1895; Neuhoff, 1924; Wheldon, 1935, 1935*A*, 1937.
[3] Wheldon, 1934. [4] Dangeard, 1895; Wheldon, 1934. [5] Coker, 1920.

fuse with each other, and the fusion nucleus divides meiotically into four daughter nuclei.[1] Even before completion of the last nuclear divisions, the young basidium (the hypobasidium) may begin to develop mamillate protuberances (the epibasidia) at the distal end.[2] However, in most cases the epibasidia do not appear until after the hypobasidium has divided vertically into four uninucleate cells (Fig. 280*E*). An epibasidium elongates until its apex projects beyond the gelatinous

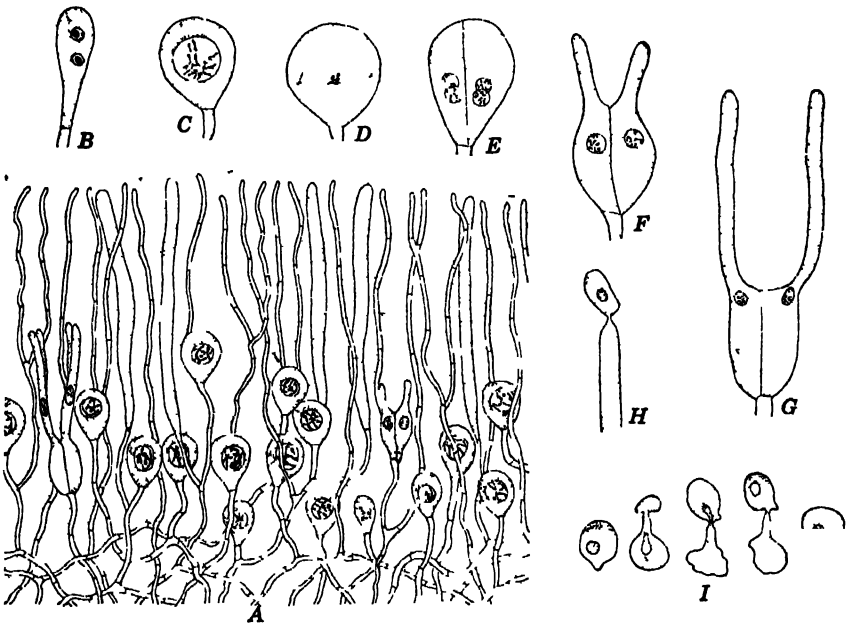


FIG. 280 —*A H, Tremella frondosa* Fries. *A*, diagrammatic vertical section of a portion of a hymenium with basidia at various stages of development *B G*, stages in the development of basidia *H*, basidiospore. *I*, formation of secondary basidiospores from basidiospores of *T. mesenterica* Retz. (*I*, *after Wheldon*, 1934.) (*A*, × 650, *B–H*, × 1,300; *I*, × 575.)

matrix of the fruiting body. Then it develops a sterigma and basidiospore at its distal end (Fig. 280*F–H*). A single nucleus moves into each elongating epibasidium and eventually migrates into the sterigma and basidiospore.[2] There is the usual explosive abscission of basidiospores from their sterigmata.[3]

A germinating basidiospore may form a short hypha with a length about that of the spore and then develop a typical basidiospore at the hyphal apex.[2] The single nucleus of the old spore remains undivided and migrates into the new spore (Fig. 280*I*). The significance of this formation of secondary basidiospores is unknown. A basidiospore may

[1] Dangeard, 1895; Maire, 1902; Neuhoff, 1924; Wheldon, 1934.
[2] Wheldon, 1934. [3] Buller, 1922.

also germinate to form a hypha composed of a few short cells that may produce clusters of small ovoid conidia.[1]

ORDER 5. AURICULARIALES

The Auriculariales have a basidium in which either the entire basidium or only the epibasidial portion is transversely divided into four cells, each of which bears a single sterigma and basidiospore. The fruiting body may have the basidia freely exposed from the beginning, or it may have them enclosed by sterile tissue before the time of spore formation. The mycelium may either be amorphous or organized into a definite fruiting body that is generally of a jelly-like consistency. Some genera are saprophytic, others are parasitic. The order includes about 15 genera and 125 species.

A haplophasic mycelium with uninucleate cells has been demonstrated for one member of the order,[2] and it has also been shown that this mycelium may reproduce by means of conidia.[3] A diplophasic mycelium with binucleate cells and clamp connections has been found in several of the genera.[4]

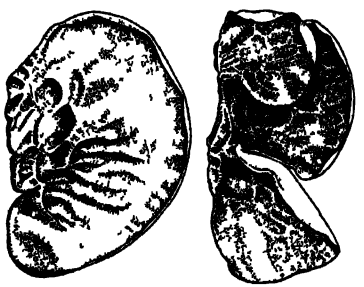


FIG. 281.—*Hirneola auricula-judae* (L.) Berk. (× ½.)

Hirneola is a saprophyte that grows on stumps or dead trunks of various trees. Its fruiting body is more or less ear-shaped and is so attached to the substratum that the concave side faces downward (Fig. 281). When moist, a fruiting body is gelatinous in texture, but it gradually changes to a horny consistency as it loses water. During rainy weather a dried-out fruiting body imbibes water, returns to the gelatinous condition, and resumes growth. Mature fruiting bodies may be up to 10 cm. in diameter.

A basidiospore shed from a fruiting body of *H. auricula-judae* (L.) Berk. divides transversely into three or four cells, and then one or more of the cells send out a hypha.[1] Such hyphae may produce clusters of sickle-shaped conidia. This may take place shortly after a hypha has emerged from the old spore wall or after it has become a much-branched mycelium. The conidia may germinate into mycelia that produce further conidia.[1] Probably, as shown for another genus of the order[2] this conidium-producing hypha is haplophasic.

Nothing is known concerning the origin of the diplophase condition in *H. auricula-judae*, but it is known that the hyphae of the mature

[1] Brefeld, 1888. [2] Shear and Dodge, 1925.
[3] Brefeld, 1888; Shear and Dodge, 1925.
[4] Shear and Dodge, 1925; Kniep, 1928; Green, 1925.

fruiting body are binucleate[1] and have clamp connections.[2] The fruiting body of this species is an intricately interwoven system of narrow hyphae in which spaces between the hyphae are filled with a gelatinous substance. The convex upper side of the fruiting body is covered with a palisade-like layer of broad, unicellular, club-shaped, sterile hyphae. Basidial development is restricted to the lower concave side. The basidia arise some distance in from the lower surface, but they eventually extend to just beneath the thallus surface. Developing basidia (Fig 282) of *H. auricula-judae*

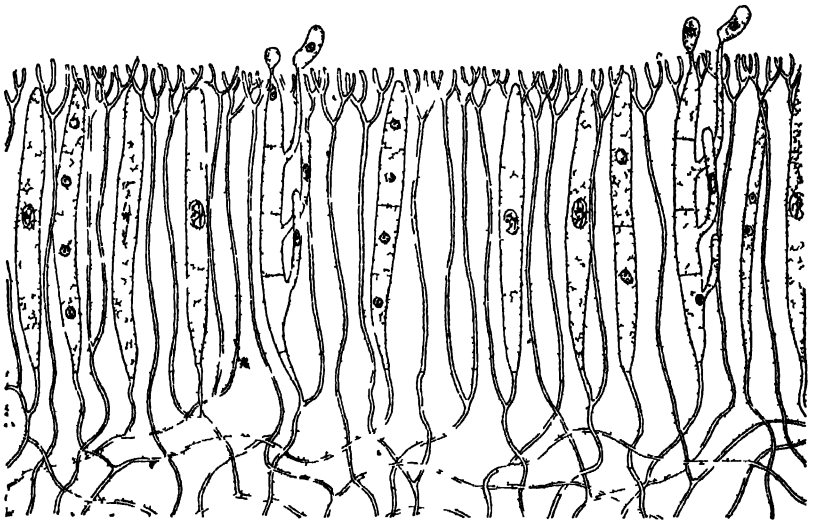


FIG 282.—*Hirneola auricula-judae* (L.) Berk. Diagrammatic vertical section of a portion of a hymenium with basidia at various stages of development (× 650)

have little if any of the differentiation into hypo- and epibasidium that is so conspicuous in many other genera of the order. The two nuclei in a young basidium unite with each other, and the fusion nucleus divides into two daughter nuclei. The basidium then becomes transversely divided into two cells,[1] each of which also divides transversely. The uppermost of the four cells develops a sterigma at its distal end; the other three cells each develop a lateral sterigma. All sterigmata grow outward, project beyond the gelatinous matrix of the fruiting body, and then form basidiospores. Abscission of a basidiospore from its sterigma is violent. If the basidium lies horizontal, the spore is hurled 0.4 to 0.5 mm. beyond the sterigma.[3]

Septobasidium is of interest because certain of its species have basidia intermediate between those of Eubasidii and Hemibasidii. A few species are known from the southeastern part of the United States, but a majority of them are found only in the tropics. The mycelium of *Septobasidium*

[1] Sappin-Trouffy, 1896. [2] Green, 1925 [3] Buller, 1922.

grows in a nongelatinous felt-like layer over portions of stems and branches of woody plants infected with scale insects. The relationship between fungus and insect seems to be symbiotic in nature rather than a case of parasitism or saprophytism.[1]

Basidiospores are the only spores formed on mycelia of most species, but the mycelium of one species[2] is known to form chains of oidia. The basidia of certain species have a conspicuous differentiation into hypobasidium and epibasidium; those of other species lack such a differentia-

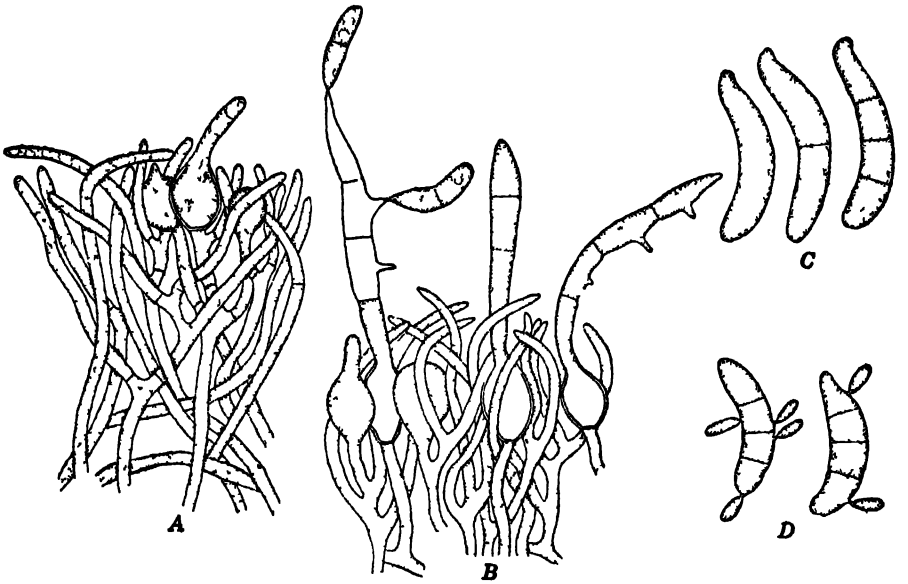


FIG 283.—*A*, *Septobasidium retiforme* (B and C) Pat Vertical section of hymenial surface with young basidia *B D*, *S pseudopedicellatum* Burt *B*, Vertical section of hymenial surface with mature basidia *C*, basidiospores *D*, basidiospores with conidia (*After Coker*, 1920) (*A–B*, × 540, *C–D*, × 1,080)

tion. *S. pseudopedicellatum* Burt is representative of the species with hypo- and epibasidium. Basidia of this species are developed at the tips of erect hyphae just beneath the surface of the mycelium.[3] A basidium is broadly ovoid, and, after it has reached a certain stage of development, it secretes a thick wall (Fig. 283*A*). When such a spore-like hypobasidium is moistened, it produces an epibasidium and basidiospores in about two days. The epibasidium is an elongate tube that extends some distance beyond the mycelium (Fig. 283*B*). It becomes transversely divided into four cells, each of which produces a single elongate and somewhat arcuate basidiospore that becomes transversely divided into about eight cells before abscission (Fig. 283*C*). Cells of a germinating basidiospore may either send forth hyphae or they may bud off small conidia.[3]

[1] Couch, 1929. [2] Patouillard, 1913. [3] Coker, 1920.

SUBCLASS 2. HEMIBASIDII

Basidia of the Hemibasidii are formed by germination of a special resting spore instead of directly upon the mycelium as in the Eubasidii. Almost all members of the subclass form one or more types of spore other than the one germinating to form a basidium. The subclass includes about 125 genera and 6,200 species. All these are parasitic on vascular plants.

The Hemibasidii have a life cycle in which there is an alternation of haplophase and diplophase. The haplophasic portion of the cycle may be reduced to one cell, but more often it is an extensive mycelium with many uninucleate cells. Conversely, the diplophase is generally composed of many binucleate cells but, as in the microcyclic rusts (page 500), it may be reduced to a single binucleate cell. Transition from haplophase to diplophase may be due to a conjugation of vegetative cells, as in smuts, or to a formation of special spores, as in macrocyclic rusts. In the latter case haplophase and diplophase are distinct from each other and either parasitic upon the same host or upon different hosts. An alternate succession of diplophase and haplophase is not obligatory in the life cycle of many Hemibasidii since there may be a formation of spores that reduplicate either the haplophase or the diplophase generations. In some cases there is a reduplication of both generations.

The Hemibasidii are generally considered more closely related to the Auriculariales than to any other Eubasidii, but there are those[1] who consider the relationship so remote that the smuts and rusts are placed in a group coordinate with Ascomycetae and Basidiomycetae.

The Hemibasidii are divided into two orders.

ORDER 1. UREDINALES

The Uredinales are obligate parasites in which the terminal cells of subepidermal hyphae develop into one- to several-celled spores (teleutospores) in which each cell is binucleate. Each cell of a teleutospore may develop into a basidium which, with a very few exceptions, becomes transversely divided into four uninucleate cells, each of which produces a basidiospore. Some species form three additional types of spore. Other species lack one, two, or all three of these additional spore types. The order includes about 100 genera and 5,000 species.

The life cycle of the Uredinales involves an alternation of a multicellular generation of many uninucleate cells (the haplophase) with a diplophase that may either consist of a single binucleate cell or many binucleate ones.

[1] Bessey, E. A., 1935; Clements and Shear, 1931.

All Uredeniales produce teleutospores. If no other binucleate spores than teleutospores are produced during the complete life cycle, the rust is said to be short-cycled or *microcyclic*.[1] If there is production of one or more additional types of binucleate spores, it is said to be long-cycled or *macrocyclic*.

Macrocyclic rusts may have the three following types of spore in addition to teleutospores and basidiospores: *Aecidiospores* which are binucleate, borne upon a mycelium that is haplophasic or began development as a haplophasic mycelium, and always produce a diplophase mycelium when they germinate. *Uredospores* which are binucleate, are always borne upon a diplophase mycelium, and always produce a diplophase mycelium when they germinate. *Spermatia* which are uninucleate, are always borne upon a haplophase mycelium, and may reduplicate the haplophase or help initiate a new diplophase. Macrocyclic rusts may be *autoecious* with the two alternating generations borne upon the same or closely related hosts or *heteroecious* with the two generations on distantly related hosts.

Teleutospores and basidiospores may be the only spores produced in the life cycle of a microcyclic rust, or there may also be a production of spermatia. In some microcyclic rusts the entire vegetative mycelium is haplophasic; in others some portions of the mycelium are haplophasic and others diplophasic.

The present tendency is to divide the Uredinales into two families[2] that differ from each other in the manner in which the teleutospores are borne.

Puccinia graminis Pers. is a macrocyclic rust in which the life cycle involves all possible types of spore. It is also heteroecious, with the haplophase parasitic on the barberry and the diplophase parasitic on wheat, oats, rye, barley, and many grasses. Although there are no evident morphological differences between spores of the diplophase from host to host, there are many biological races within the species. Thus, uredospores from stems of the wheat will not readily infect oats, rye, or barley. In addition, there are also biological races upon the same host, and at least 37 physiological forms have been distinguished[3] in 12 agronomic varieties of wheat.

Infection of wheat with *P. graminis* is externally evident because of the vertically elongate, reddish-brown or blackish, granular pustules upon the stem and leaves. The first pustules (*sori*) appear late in spring and are reddish-brown. Since they contain uredospores only, they are known as *uredosori*. The uredospores of a uredosorus are freely exposed, and they may become detached and carried to other plants by the

[1] Arthur and Kern, 1926; Arthur *et al.*, 1929. [2] Arthur, 1934; Dietel, 1928.
[3] Stakeman and Levine, 1922.

wind. A uredospore is broadly ovoid, binucleate, and with four or five circular thin areas (*germ pores*) in the relatively thick wall. It germinates within a few hours after falling upon a suitable host plant and sends out a hypha (*germ tube*) through one or more of the germ pores (Fig. 284*A*). If it sends out two germ tubes, one grows more vigorously than the other. A germ tube grows over the surface of the epidermis of the host and, when it reaches a stoma, its tip develops into an elongate vesicle—the *appressorium*. The binucleate protoplast of the germ tube migrates into the appressorium, and the empty germ tube becomes separated from the appressorium by a cross wall [1] The appressorium then sends downward a wedge-like outgrowth whose distal end usually enlarges into a vesicle after it has grown through the stomatal slit The contents of the

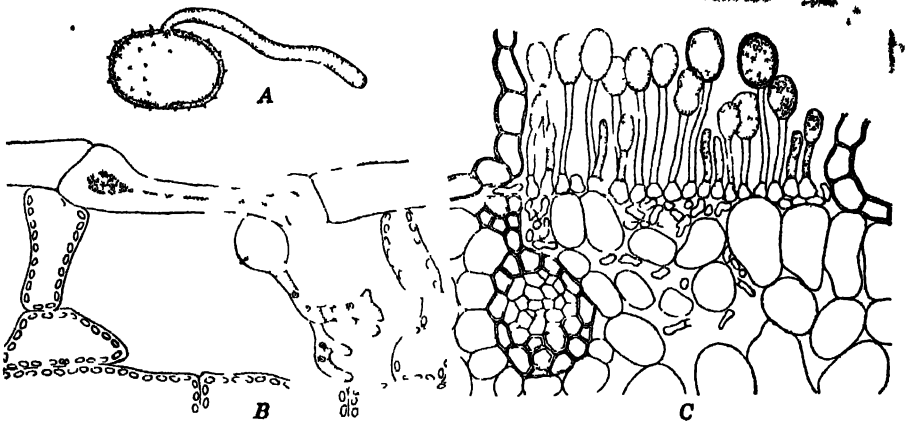


FIG 284.—*Puccinia graminis* Pers 1, germination of a uredospore *B*, infection of a wheat plant by growth of a hypha through a stoma *C* uredosorus (*A*, × 650, *B*, × 485, *C*, × 325)

appressorium migrate into the vesicle developed beneath the stoma, and a much-branched mycelium, composed of many short binucleate cells, then grows from the substomatal vesicle (Fig. 284*B*). Growth of the mycelium is intercellular and with a formation of many short haustorial branches that penetrate the host cells A fully developed mycelium does not extend far from the point of entrance into the host. There is some killing of host cells in the infected area, but many of them appear to be normal. Hyphal branches of the mycelium are especially numerous just beneath the epidermis of the host, and within five or six days they begin to form uredospores. The first uredospores mature 10 to 12 days after infection. A very young uredosorus consists of a layer of binucleate *basal cells* that elongate vertically and divide transversely (Fig. 284*C*). The inferior daughter cell, which does not divide, is the *foot cell*. The superior daughter cell divides transversely, the upper daughter cell

[1] Allen, 1923.

maturing into a uredospore and the lower one into a *stalk cell*. Since there is a continual differentiation of new basal cells in a sorus, there may be a long-continued production of uredospores. Maturation of the first uredospores is followed by a rupturing of the overlying epidermis of the host and dispersal of the uredospores. The time interval between infection and development of the new mycelium to a fruiting condition is so short (10 to 12 days) that several successive generations of uredo-

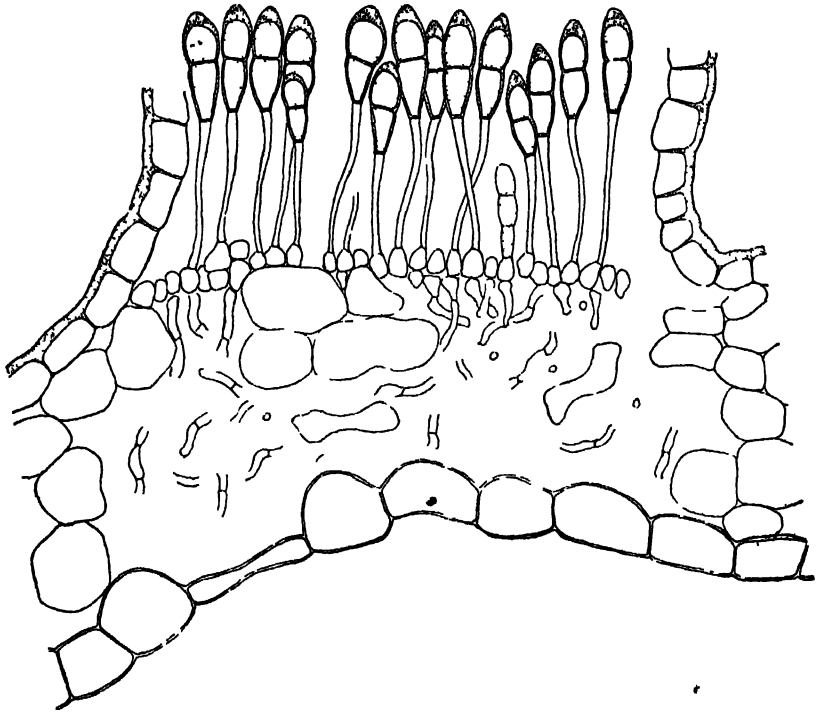


FIG 285.—*Puccinia graminis* Pers Vertical section through a teleutosorus (× 325)

spore-producing mycelia may be formed during the summer if conditions are favorable.

Toward the end of summer, the mycelium begins to produce teleutospores instead of uredospores. The first teleutospores are generally developed in a sorus containing uredospores; sori produced late in the development of the host contain only teleutospores. The change from uredo- to teleutospore production is dependent upon the photosynthetic activity of the host, and it has been shown[1] that under certain conditions there may even be a reversal from teleuto- to uredospore production. Teleutospore development is similar to uredospore development except that the sister cell of the stalk cell divides into two binucleate cells which develop into a two-celled teleutospore (Fig. 285). Both cells of the

[1] Waters, 1928.

teleutospore secrete a thick wall containing a single germ pore. Both cells have the two nuclei unite with each other as the spore wall matures.[1]

Ordinarily the teleutospores do not germinate until the next spring. At this time they may either be lying on the ground or still be attached to the old sorus. One or both of the cells of a germinating teleutospore send forth a tubular outgrowth (the epibasidium) that becomes transversely divided into four uninucleate cells. The nuclear behavior is unknown in *P. graminis*, but another species of *Puccinia* is known[2] to have the fusion nucleus migrating into the epibasidium and there dividing meiotically into four daughter nuclei. Transverse walls are formed after both the first and the second nuclear divisions. Each cell of the epibasidium of *P. graminis* forms a lateral sterigma and basidiospore, but this generally takes place in the median cells before it does in the terminal ones (Fig. 286*A*). As in the Eubasidii,[3] abscission of basidiospores is explosive.

Basidiospores are incapable of infecting wheat, and they can only develop into a mycelium if they fall upon a barberry. A basidiospore falling upon a leaf or a young twig of the barberry sends out a germ tube that grows directly through the outer wall of an epidermal cell and there forms a hypha of four to six uninucleate cells.[4] Branches grow out from each cell of this hypha, and they develop into a much branched haplophasic mycelium that grows between all cells between the lower and upper epidermis of a leaf. About the fourth day after infection, dense mats of hyphae appear here and there between the upper epidermis and the palisade tissue. These are the primordia of the *spermogonia* or *pycnia* (Fig. 286*B*). The mat-like primordium of a spermogonium soon sends up numerous erect branches that converge to a common point and push up the overlying epidermis. The spermogonium eventually becomes flask-shaped and forms a pore-like opening, the *ostiole*. Hyphae adjacent to the ostiole develop into sterile paraphyses; those lining the spermogonium terminate in elongate uninucleate cells each of which cuts off a succession of small spore-like bodies (*spermatia*) at the distal end. The spermatia accumulate in a large droplet of nectar-like liquid exuded through the ostiole. It is extremely doubtful if spermatia can reinfect the barberry and thus reduplicate the haplophase. Until quite recently the spermatia were thought to be spores that have become functionless. It is now known that *P. graminis* is heterothallic[5] and that the spermatia are an essential factor in inducting a return to the diplophase condition. Unlike most other heterothallic basidiomycetes, *P. graminis* has no conjugation when two haploid mycelia of opposite sex come in contact with each other. Instead, the diplophase is initiated by a transfer of sperma-

[1] Sappin-Trouffy, 1896. [2] Allen, 1933. [3] Buller, 1924. [4] Allen, 1930.
[5] Craigie, 1927, 1927*A*, 1928, 1931

tia from a spermogonium of one sex to another of the opposite sex,[1] or by a spermatium coming in contact with a vegetative hypha of the opposite sex.[2] Under natural conditions intermingling of spermatia of opposite sexes may take place when two spermogonia develop close to each other and the exudates flow together, or it may result from insects carrying a droplet of spermogonial exudate to another spermogonium.[3]

Cytological investigation shows[2] that there is often a fusion between spermatia and vegetative hyphae that have pushed up through and

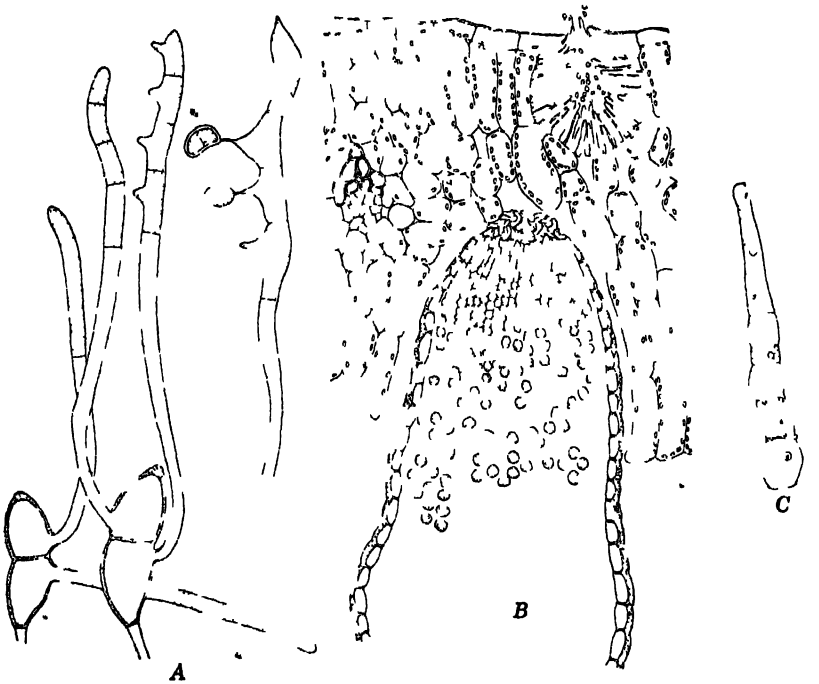


FIG 286.—*Puccinia graminis* Pers. *A*, formation of epibasidia by germinating teleutospores. *B*, vertical section of a barberry leaf showing a spermogonium and an aecidium. *C*, a chain of aeciospores alternating with small sterile cells. (*A*, × 480, *B* × 160, *C*, × 650.)

projected beyond the upper epidermis. Two lines of evidence indicate that spermatium and hypha are of opposite sexes. One is the lack of fusion and continued formation of spermatia if the leaf is inoculated with a single basidiospore. The other is the immediate cessation of spermatial formation, the drying up of the exudate, and the death of the spermogonia if fusion does take place.

It is uncertain how the diplophase initiated at the upper surface reaches the lower surface of a leaf. It may be either by a migration of nuclei through hyphae of the haplophase mycelium or by a downward

[1] Craigie, 1927, 1927*A*. [2] Allen, 1933. [3] Craigie, 1927*A*, 1928, 1931.

growth of binucleate hyphae. In any case, there is a loosely interwoven snarl of hyphae between the lowermost mesophyll cells. Some of the cells are binucleate; others are uninucleate.[1] A palisade-like layer of binucleate cells is eventually differentiated from the snarl, and each cell functions as a basal cell that cuts off a succession of binucleate cells, each of which immediately divides transversely into a large and a small daughter cell. The large cell becomes an *aecidiospore;* the smaller one disintegrates (Fig. 286*C*). The margin of the spore-forming area is encircled by a ring of basal cells each of which cuts off a succession of binucleate cells that do not redivide into large and small cells. Instead they develop into a protective layer, the *peridium,* in which the radial and outer tangential walls are greatly thickened. The peridium and the chains of aecidiospores jointly constitute the *aecidium* (Fig. 286*B*). The apex of the peridium eventually ruptures, and the binucleate aecidiospores are liberated from the cup-like aecidium.

Aecidiospores are shed late in the spring. They cannot reinfect the barberry, but, if one of them is carried to a wheat plant, it may germinate and send forth a hypha that grows through a stoma. The mycelium developed within tissues of the wheat is composed of binucleate cells, and within 10 to 12 days it begins to form uredospores.

In a typical life cycle of *P. graminis,* the first infection of a young wheat plant is by means of aecidiospores. However, this is not always the case, and the first infection may be either by uredospores that have survived over winter or by uredospores that have been carried by winds from regions where the rust has already begun the production of uredospores.

The microcyclic rusts are generally interpreted as types that are derived from, instead of more primitive than, the macrocyclic rusts. Some microcyclic rusts derived from macrocyclic rusts have had an obliteration of all types of spore but the teleutospore and basidiospore; others have had an obliteration of all spore types but the teleutospore, basidiospore, and the spermatium.

Puccinia malvaccarum Bert., the hollyhock rust, is representative of microcyclic rusts which form only teleutospores and basidiospores. Its mycelium is haplophasic in the first-developed portion[2] and diplophasic in the portion bearing the teleutospores. Development of teleutospores[3] is similar to that in *P. graminis,* and the two nuclei in both cells of a teleutospore fuse with each other before the spore is ripe (Fig. 287*A–C*). Germination may take place immediately after ripening of a spore, and both cells generally send forth an epibasidium. The fusion nucleus migrates into the epibasidium, and there undergoes meiosis.[3] Transverse cross walls are formed between daughter nuclei of both the

[1] Allen, 1930. [2] Ashworth, 1931; Allen, 1935. [3] Allen, 1933*A*.

first and the second nuclear divisions (Fig. 287*E*). Each of the four cells sends forth a sterigma and develops a basidiospore at the sterigmatal apex (Fig. 287*F–G*). The basidiospores are formed in acropetalous succession instead of simultaneously. Each basidiospore is uninucleate before germinating. The basidiospore immediately infects the host, and the mycelium developing from it soon produces teleutospores. Thus several successive generations of the fungus may develop during a single growing season of the host.

Evolution of a short-cycled type of rust does not always center around the teleutospore. The microcyclic "orange rust" of the black-

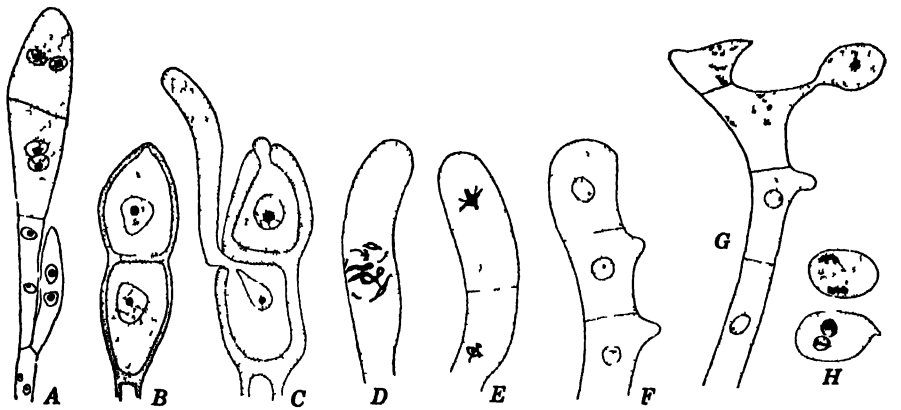


FIG. 287.—*Puccinia malvacearum* Bert. *A*, young teleutospore. *B*, mature teleutospore. *C–G*, stages in development of epibasidia by germinating teleutospores. *H*, basidiospores. (*After Ruth F. Allen*, 1933.) (*A–C*, × 700, *D–H*, × 1,125.)

berry (*Rubus*) illustrates this. There are two orange rusts on *Rubus*, and the two are indistinguishable from each other at the so-called *caeoma stage*.[1] One of them [*Gymnoconia Peckiana* (Howe) Trotter] is macrocyclic and produces spermatia, teleutospores, basidiospores, and aecidiospores. Its aecidiospores are borne in the type of naked aecidium known as a *caeoma*. The other orange rust [*Kunkelia nitens* (Schw.) Arth.] is microcyclic and only develops spermogonia in addition to a caeomoid type of fructification. *K. nitens* was distinguished[2] from *G. Peckiana* shortly after the discovery[3] that germinating spores from its caeoma produced typical epibasidia and basidiospores. In the United States, *G. Peckiana* is found on species of *Rubus* growing east of the Mississippi and north of the Ohio rivers. *K. nitens* is found both on *Rubus* growing south of the Ohio and on *Rubus* growing along the Pacific Coast.[2]

Basidiospores of *K. nitens* sprayed onto leaves of *Rubus* cause a typical infection.[4] There is also an infection when teleutospores are sprayed onto a leaf, but it is uncertain whether they infect the leaf directly or

[1] Kunkel, 1916. [2] Arthur, 1917. [3] Kunkel, 1914. [4] Dodge, 1923.

germinate to form basidiospores. The mycelium developed within the leaf is haplophasic and intercellular. In most cases the mycelium produces both spermogonia and caeoma. Development of spermogonia may take place prior to or simultaneously with that of the caeoma. Caeomal development begins with the differentiation of a palisade-like layer of hyphae just within the lower epidermis. This layer eventually gives rise to vertical chains of binucleate cells in which large and small

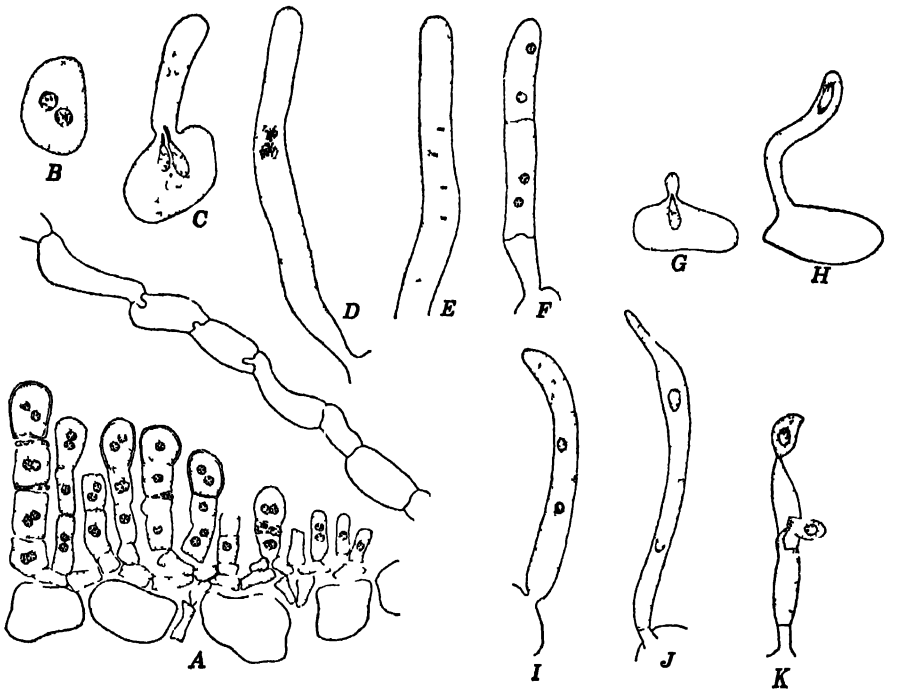


FIG. 288.—*Kunkelia nitens* (Schw.) Arth. *A*, vertical section of a portion of a caeoma. *B*, binucleate spore from a caeoma. *C–F*, successive stages in germination of binucleate spores. *G–K*, successive stages in germination of uninucleate spores and their production of basidiospores. (*B–K, after Dodge and Gaiser*, 1926.) (*A*, × 430.)

cells alternate with one another just as in the aecidium of *Puccinia graminis* (Fig. 288*A*). The origin of the binucleate condition is uncertain. It has been described[1] as being due to a lateral fusion of two uninucleate cells cut off at the distal end of two adjoining haplophasic hyphae. It has also been ascribed to a fusion of spermatia and vegetative hyphae, just as in *P. graminis*.[2] One is inclined to accept the latter interpretation since it has been shown[1] that there is no production of binucleate spores unless the mycelium has also developed spermogonia. If there are no spermogonia, there is a formation of chains of uninucleate spores in the caeoma.[1]

[1] Dodge, 1924. [2] Forsberg, in E. A. Bessey, 1935.

Spores of a caeoma are identical in external appearance with the aecidiospores formed in a caeoma of *Gymnoconia Peckiana*. However, the spores from a caeoma of *K. nitens* should be interpreted as teleutosporic in nature since they are binucleate and germinate to form typical epibasidia. Binucleate caeomid spores of *K. nitens* have no fusion of the two nuclei either before or after germination.[1] The germinating spore sends out a tubular epibasidium, and the two nuclei migrate into it (Fig. 288*B–F*). Shortly afterward a cross wall is formed between the two nuclei. Each uninucleate cell generally divides into two daughter cells, but sometimes there is a formation of more than four cells in the epibasidium. Each cell of the epibasidium then forms a basidiospore in the usual manner. Germinating uninucleate teleutospores (Fig. 288*G–K*) generally have the epibasidium dividing transversely into two cells each of which produces a basidiospore, but there may be a formation of more than two cells.[2]

ORDER 2. USTILAGINALES

The Ustilaginales (smuts) are parasites in which intercalary cells of the binucleate mycelium form binucleate chlamydospores. The chlamydospores germinate directly into septate or unseptate epibasidia. The order includes about 30 genera and 600 species.

The Ustilaginales are divided into two families that differ from each other in structure of the epibasidium

FAMILY 1. USTILAGINACEAE

The Ustilaginaceae have the germinating chlamydospore producing an epibasidium that becomes transversely divided into uninucleate cells. Each cell of the epibasidium may form an indefinite number of basiodiospores. There are about 12 genera and 350 species.

Ustilago has about 300 species and most of them are parasitic upon a single host species. Certain species of *Ustilago* are parasitic upon cereals. These are of considerable economic importance since they may reduce the yield of grain by 25 to 50 per cent. The corn smut [*U. Zeae* (Beckm.) Ung.] generally infects the ears or tassels of a corn plant (Fig. 289), but it may infect the stem, leaves, or aerial roots. Infection may take place at any time during the growing period of the host.

Infection is by means of basidiospores or by conidia produced by budding of basidiospores. *U. Zeae* is heterothallic, and a typical infection with production of chlamydospores is dependent upon inoculation with two basidiospores or two conidia of opposite sex.[3] Each basidiospore

[1] Dodge, 1924. [2] Dodge, 1924; Dodge and Gaiser, 1926.
[3] Hanna, 1929; Sleumer, 1931; Stakeman and Christensen, 1927.

or conidium sends out a hypha that immediately grows through the epidermis of the host and then continues growth horizontally beneath it. Conjugation may take place immediately after penetration (Fig. 290*A*), but more frequently each spore produces a haplophase mycelium of a few uninucleate cells before conjugation takes place.[1] When the host is infected with a single spore or with several spores of the same sex, there is a formation of a many-celled haplophase mycelium, but this never produces chlamydospores nor induces a formation of galls by the host.[2]

The diplophase mycelium extends to only a limited distance from the point of infection (Fig 290*B*). It grows chiefly in intercellular spaces of the host tissue and sends short haustorial branches into the host cells. The presence of clamp connections in the diplophase has been affirmed[2] and denied.[3] The latter interpretation seems to be the correct one since the available evidence[4] seems to show that the number of nuclei in various cells of the diplophase ranges from one to a dozen or more. Ordinarily the diplophase produces only chlamydospores, but under exceptional circumstances certain hyphal branches may protrude through the epidermis of the host and form conidia. These conidia are always uninucleate, and they are incapable of developing into a chlamydospore-producing mycelium when reinoculated on the host.[2]

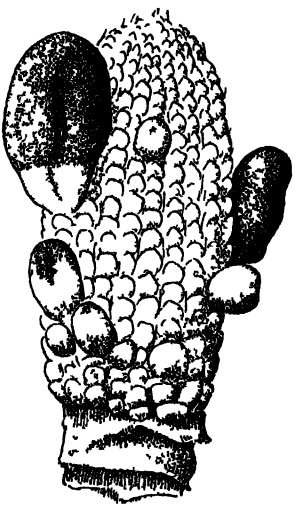


Fig. 289. An ear of corn infected with *Ustilago Zeae* (Beckm.) Ung. ($\times \frac{2}{3}$)

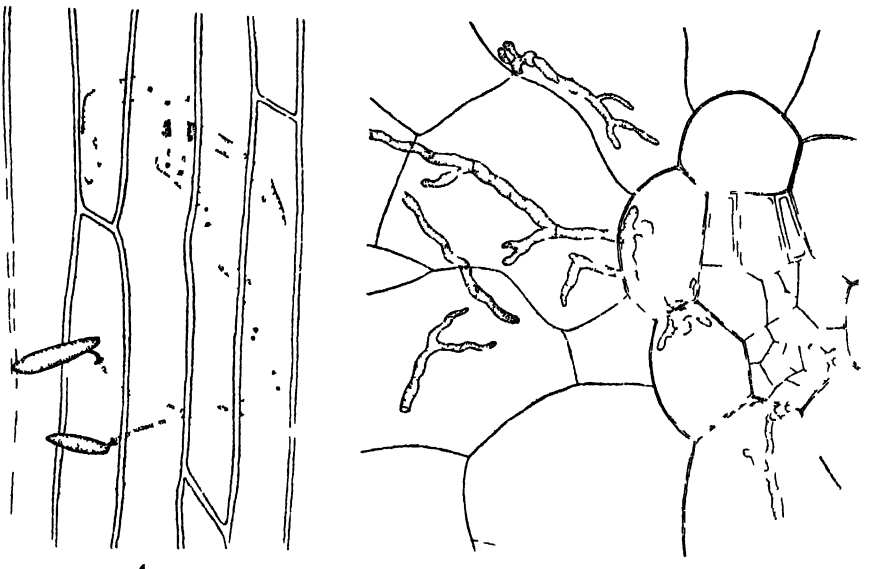
The presence of the mycelium in the host induces an active division and redivision of cells in the infected region, and many of them increase to an enormous size. This causes a gall-like swelling of the infected region and one that may be up to 10 cm. in diameter. Eventually there is a death of all host cells below the epidermis of the gall.

Branches of the mycelium of *U. Zeae* are so densely entangled with one another that the details of chlamydospore formation cannot be made out with certainty. However, it is known that the cells developing into chlamydospores are binucleate.[1] In certain other species, as *U. Vuijckii* Oud. and Beij.,[5] every cell throughout the length of a hypha produces a chlamydospore. The two nuclei in a young chlamydospore of *U. Zeae* unite with each other, and the protoplast becomes rounded and secretes a thick wall. The gall now consists of an epidermal layer overlying a powdery mass of innumerable chlamydospores intermingled with dried

[1] Hanna, 1929; Sleumer, 1931. [2] Hanna, 1929. [3] Sleumer, 1931.
[4] Lutman, 1910; Sleumer, 1931. [5] Seyfert, 1927

remains of host cells and sterile hyphae. The epidermis of the host may dry out and rupture any time after the spores are mature.

Chlamydospores of *U. Zeae* may germinate immediately after they are shed, but it is very probable that a majority of them do not germinate until the spring following their formation. A germinating chlamydospore of *Ustilago* sends out a short tubular outgrowth, the epibasidium (Fig 291). In *U. Zeae* the fusion nucleus divides into two daughter nuclei, one of which migrates into the epibasidium Each nucleus divides again,



A *B*

FIG 290.—*Ustilago Zeae* (Beckm.) Ung. *A*, surface view of a corn leaf containing a diplophase mycelium formed by conjugation of hyphae from two germinating conidia. *B*, vertical section of a corn leaf showing a mycelium growing through hypertrophied host tissues (*A*, *After Hanna*, 1929) (*A*, × 540, *B*, × 650)

and one or both daughter nuclei of the nucleus within the old spore wall also migrates into the epibasidium [1] The three- or four-nucleate epibasidium then becomes transversely divided into four uninucleate cells The nucleus of each epibasidial cell divides into two daughter nuclei. One of them migrates into a basidiospore budding off from the cell; the other remains within the cell. Ordinarily the nucleus remaining within the cell divides again, and there is a budding off of a second basidiospore (Fig. 291*E*). This may be repeated indefinitely. Genetic analyses[2] show that division of the fusion nucleus is reductional and that two cells of the epibasidium produce basidiospores of one sex and the other two produce basidiospores of the opposite sex. The chances for an infection

[1] Hanna, 1929

[2] Hanna, 1929; Holton, 1932; Sleumer, 1931; Stakeman and Christensen, 1927.

of the host are greatly increased because of the budding off of conidia from the basidiospores. This may take place before or after detachment of a basidiospore from the epibasidium.

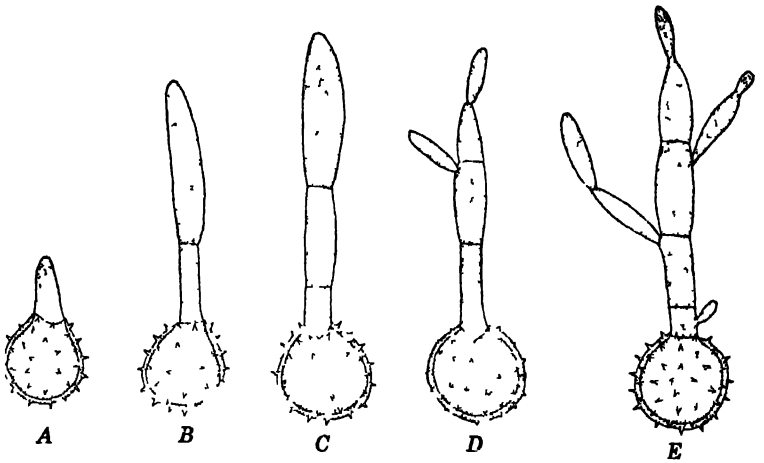


FIG. 291.—*Ustilago Zeae* (Beckm.) Ung. Stages in the formation of epibasidia by germinating chlamydospores and the production of conidia by the budding of basidiospores. (× 1,300.)

FAMILY 2. TILLETIACEAE

The Tilletiaceae have the germinating chlamydospore producing an epibasidium that does not become transversely divided into uninucleate cells. The epibasidium produces a definite number of basidiospores, and all of them are borne at its distal end. There are about 13 genera and 250 species in the family.

Tilletia is a genus with about 40 species. Two of these [*T. Tritici* (Bjerk.) Wint. and *T. foetans* (B. & C.) Trel.] are parasitic on wheat. Collectively they form the disease known as *bunt*. This is not a serious disease in this country except in the Pacific Northwest. Heads of wheat infected with bunt have an odor resembling that of decaying fish.

Infection of the host can only take place during the seedling stage. If chlamydospores are used as the inoculum, there is a high percentage of infection by *T. Tritici* for the first six days after the seeds are planted and none after the tenth day.[1] If conidia are used as the inoculum, there is considerable infection for the first eight days and none after the twelfth. Development of the mycelium within a seedling keeps pace with that of the host tissues. A mycelium growing within a host does not give external evidence of its presence, and it is impossible to distinguish between infected and uninfected individuals until the host begins to flower. At this time there is a rapid development of hyphae in the

[1] Sartoris, 1924.

floral organs Flowers of infected plants have ovaries about twice the normal size and have stamens that are reduced and abortive.[1] At the time when the grain of uninfected plants is ripening, there is a replacement of the ovules of infected plants by a mass of chlamydospores. The

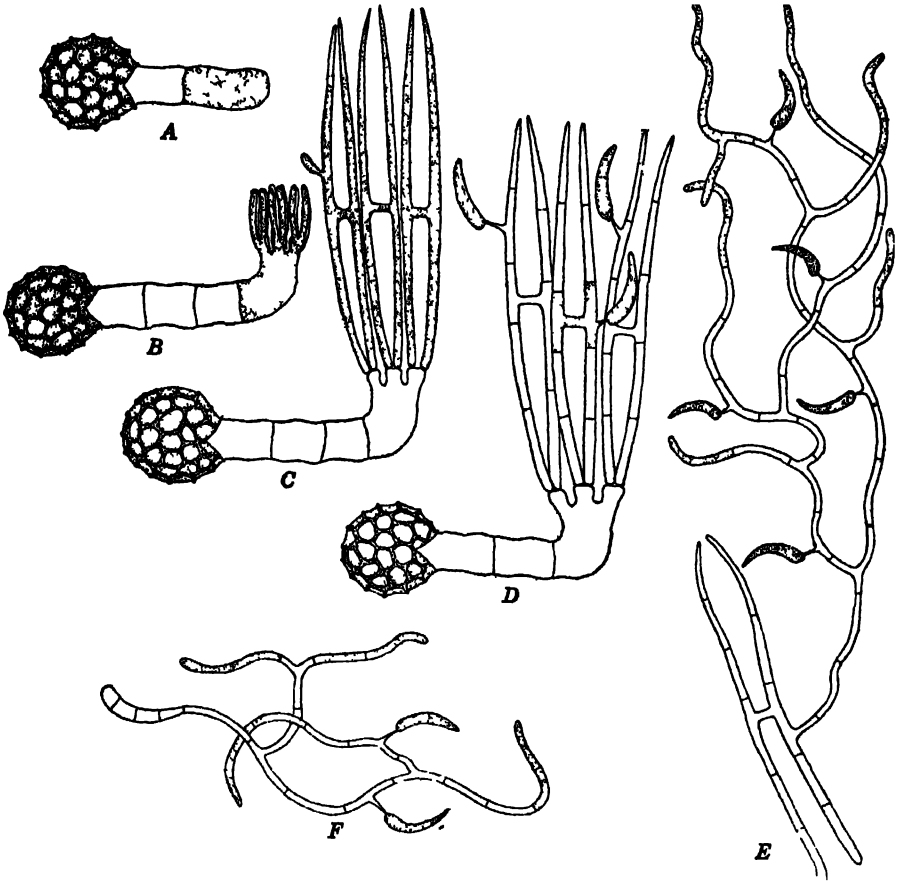


FIG 292.—*Tilletia Tritici* (Bjerk) Wint *A B*, diagrams showing the formation of epibasidia by germinating chlamydospores and the formation of basidiospores *C–D*, diagrams showing the conjugation of basidiospores and the formation of conidia *E* diagram showing the development of a mycelium and conidia from a conjugated pair of basidiospores *F*, diagram showing the production of secondary conidia after germination of a primary conidium (*Diagrams based upon Buller*, 1933) (× 300)

ovary walls in infected plants mature into "seed coats" just as in normal kernels, and the resultant kernels, filled with chlamydospores, are known as *smut balls*. Under natural conditions it is very probable that the seed coat of the smut ball remains intact until the following spring. When wheat is cultivated as a crop plant, there is a breaking of a certain percentage of the smut balls as the wheat passes through the threshing

[1] Barrus, 1916.

machine. Many of the chlamydospores from these broken smut balls lodge upon normal kernels passing through the machine and are sown with the grain when the next crop of wheat is planted.

Germinating chlamydospores of *Tilletia* contain a single fusion nucleus, and it migrates into the epibasidium developing from the chlamydospore. The fusion nucleus generally divides and redivides into eight daughter nuclei, but it may divide to form more than eight.[1] As the epibasidium elongates (Fig. 292*A–B*), its protoplasm becomes restricted to the distal end and successive septa are laid down as the basal portion is evacuated.[2] Eight to 24 elongate acicular basidiospores, each with one nucleus, are developed at the distal end of the epibasidium. Half of these spores are of one sex and half of the other.[3] Conjugation takes place at the basidiospore stage and either before or after abscission of the basidiospores (Fig. 292*C*). After establishment of the conjugation tube, the protoplast of one basidiospore migrates into the other,[4] and transverse septa are laid down in evacuated portions of a conjugating pair of basidiospores (Fig. 292*D*). The binucleate cell produced by conjugation may form a single sickle-shaped conidium, or it may send forth a single branching many-celled hypha[2] that bears several conidia (Fig. 292*E*). Conidia produced by conjugated cells or by a hypha growing from them may produce secondary conidia (Fig. 292*F*). Conidia, whether primary or secondary, are binucleate.[5] Their abscission is by a forcible discharge similar to that of basidiospores from basidia of Eubasidii.[6] Because of this similarity in method of discharge, it has been held[6] that the conidia of *Tilletia* are really the basidiospores. Germinating conidia send out a hypha, and infection of the host is by a direct penetration of the hypha between the epidermal cells of the host.[7] The mycelium developed within the host is diplophasic, but many of its cells may be multinucleate.[8]

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[1] Dastur, 1921; Paravicini, 1917; Dangeard, 1892; Rawitscher, 1914.
[2] Buller, 1933. [3] Flor, 1932.
[4] Dastur, 1921; Dangeard, 1892; Paravicini, 1917; Rawitscher, 1914.
[5] Boss, 1927; Dangeard, 1892; Rawitscher, 1922.
[6] Buller and Vanterpool, 1925; Buller, 1933.
[7] Sartoris, 1924. [8] Dastur, 1921; Boss, 1927.

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CHAPTER XIV

FUNGI IMPERFECTI

The imperfect fungi include those fungi in which there is neither a formation of zygotes, nor ascospores, nor basidiospores at any known stage in the fungi. They are the fungi in which the "perfect stage" (that is, zygote, ascus, or basidium) has not been discovered or is lacking. The class is wholly artificial and is erected for the temporary reception of species pending discovery of structures showing that they belong either to Phycomycetae, Ascomycetae, or Basidiomycetae. The Imperfecti also include certain fungi that never form spores at any stage of their development. These *Mycelia Sterilia* are only recognizable when they are of a distinctive type, as sclerotia, or grow in distinctive habitats, as in the case of certain mycorhizal fungi.

According to the strictest interpretation, the Imperfecti should also include phycomycetes known only in the sporangial stage; rusts in which only the aecidiospores or uredospores are known; and certain species of ascomycetous genera, as *Penicillium*, which are known only in the conidial stage. However, such fungi known only in the imperfect stage have such characteristic fructifications that there is little doubt concerning their proper systematic position.

Removal of species from the Imperfecti has been going on for more than a century. Examples of this are seen in the demonstration that *Sphacelia segetum* Lev. is the conidial stage of *Claviceps purpurea* (Fries) Tul. (page 453) and that *Fusicladium dendriticum* (Wallr.) Fcl. is the conidial stage of *Venturia inaequalis* (Cooke) Wint. (page 456). However, the list of imperfect fungi is continually expanding because new species are being added more rapidly than old ones are being removed. At present about 1,200 genera and 24,000 species are referred to the Fungi Imperfecti.

It is very probable that almost all of the fungi assigned to the Imperfecti are ascomycetes. The evidence for this includes the similarity between their conidial stages and those of Ascomycetae, the lack of unseptate mycelia characteristic of Phycomycetae, and the lack of clamp connections found in the Basidiomycetae. Sooner or later there will be a discovery of the "perfect stage" of certain species now referred to the Imperfecti. On the other hand, one cannot assume that there will be an eventual transfer of all species from the class because it is very

probable that many species have lost the ability to form the perfect stage.

The imperfect fungi include many species that cause serious diseases among plants and animals. Examples of the former are the anthracnose of beans, the leaf spot of beets, and the early blight of potatoes. The much-publicized "athlete's foot" is an example of a disease of man caused by an imperfect fungus.

Attempts have been made to arrange the Imperfecti according to a natural system, but these have been founded upon such inadequate bases that there is no assurance that they show the real phyletic relationships. For this reason it is better to follow the widely used and purely artificial system that divides the Imperfecti into orders differing from one another in the manner in which the spores are borne. These are:

Moniliales in which the conidia are borne directly upon an undifferentiated mycelium or upon specialized conidiophores. The conidiophores may be simple or compound and solitary or adjacent to one another. When the conidiophores are adjacent, they never lie in an acervulus (page 416) or in a pycnidium (page 416). There are about 600 genera and 9,000 species.

Melanconiales in which the fungi are parasitic and with the conidiophores in a subepidermal or subcortical acervulus. The order includes some 80 genera and 2,100 species.

Sphaerosidales in which the conidia are borne in a pycnidium or in a modified type of pycnidium. There are about 500 genera and 12,500 species.

Mycelia Sterila in which there is no formation of spores, and in which the mycelium has a characteristic structure or mode of growth. About 20 genera and 350 species are placed in this order.

CHAPTER XV

LICHENS

A lichen consists of two different plants, a fungus and an alga, so associated with each other that they appear to be a single plant. The fungus always envelops the algal component of the association, and the "plants" resulting from combined growth of the two are more or less constant in form and in internal structure. There are some 400 genera and 15,500 species of lichens.[1]

Every individual of a given lichen species contains the same alga and the same fungus. In three genera the fungal component is a basidiomycete; in all others it is an ascomycete. The algal component may belong to the Myxophyceae or to the Chlorophyceae and may be filamentous or nonfilamentous. Lichens have also been described in which fungi are associated with autotrophic bacteria (purple bacteria),[2] but it has also been held[3] that these bacteria are not an essential component of these lichens.

The relationship between alga and fungus in a lichen is still a matter of controversy. Some hold that "a lichen is a fungus which lives during all or a part of its life in parasitic relation with the algal host and also sustains a relation with an organic or an inorganic substratum"[4] The strongest argument that the relationship between fungus and alga is one of parasitism is the demonstration that haustorial hyphal branches or appressoria penetrate the algal cells of certain lichens. Several of those who consider the fungus a parasite place the lichens among Ascomycetae and Basidiomycetae according to the nature of the fungus.[5] Those who follow this practice hold that the algal component may be neglected and that the species name given the lichen applies only to its fungal component.

In most cases the two organisms seem to derive mutual benefit from their association. The fungus absorbs and retains moisture necessary for the partnership; the alga synthesizes the necessary carbohydrates. Thus the relationship appears to be one of symbiosis rather than one of parasitism. The symbiosis is of the type known as *helotism* because the partnership is decidedly at the expense of the alga. Those who consider the lichens a more or less symbiotic partnership place them in a class

[1] Zahlbruckner, 1922–1932. [2] Uphof, 1925, 1926. [3] Suessenguth, 1926.
[4] Fink, 1913. [5] Bornet, 1873; Fry, 1928; Geitler, 1937.
[6] Bessey, 1935; Clements and Shear, 1931.

distinct from both fungi and algae. They hold that a name given to a lichen applies to the partnership (*consortium*) rather than to the fungus. However, they recognize that in the strictest sense both the fungi and the algae should be classified separately. This is simple in the case of the algae since all of them may be referred to free-living genera of algae. Sometimes the alga within the lichen is identical with a free-living species of the genus, sometimes it is not. The fungal components cannot be referred to genera of fungi not found in lichens. To be strictly logical one would have to propose a new set of names for the fungi found in lichens. This has never been attempted.

Lichens grow on a wide variety of substrata, including the leaves and bark of trees, soil, and rocks. In most cases a given species is restricted to a particular substratum. Many lichens thrive and multiply in habitats where other vegetation is practically nonexistent. Such habitats include bare rocks and extremely cold regions. The best example of the latter is the Arctic Tundra where large areas are covered with "reindeer moss" (*Cladonia rangifera* Web.) that grows in clumps 15 to 30 cm. in height. Other lichens, especially those growing on leaves and the back of trees, thrive best when there is an abundance of moisture. This is well exemplified by the luxuriant development of lichens in tropical rain forests and in the restriction of the "Californian Spanish Moss" (*Ramalina reticulata* Kremp.) to trees growing in the more humid canyons of the Coast Range.

Lichens are of considerable ecological importance as pioneers in colonization of rocky habits by plants. Growth of a lichen upon a cliff or boulder is accompanied by a disintegration of the rock immediately beneath it. If the rock is a limestone there is more or less dissolving of the stone. Several lichens growing on limestone are endolithic and with all the vegetative cells embedded in the rock.[1] Disintegration of rocks other than limestone is almost wholly mechanical. This has been ascribed[2] to varying stresses and strains induced by expansion and contraction of the gelatinous body of the lichen. When a lichen dies, its decaying remains, together with rock particles, form a soil in which other plants may grow. The first successors are generally mosses, but sooner or later vascular plants begin to grow in the soil.

The lichens are divided into the following two subclasses:

Ascolichenes in which the fungal component is an ascomycete.

Basidiolichenes in which the fungal component is a basidiomycete.

SUBCLASS 1. ASCOLICHENES

In all but three genera of lichens the fungus associated with the alga is an ascomycete. Certain of the Ascolichenes have a thallus in

[1] Fry, 1922. [2] Fry, 1924, 1927.

which alga and fungus are uniformly distributed throughout a gelatinous or nongelatinous plant body. These lichens are always *crustose* and with the thallus forming an incrustation that adheres closely to the substratum. Other crustose lichens have an internally differentiated thallus and one in which the algae are restricted to a definite portion of the plant body (Fig. 293*A*). Lichens with an internally differentiated thallus may also be *foliose* and have a leaf-like lobed to deeply incised thallus that is attached to the substratum by rhizoid-like outgrowths (*rhizines*) from the undersurface (Fig. 293*B*). A rhizine may consist of a single simple to branched hypha or of a number of parallel hyphae that lie closely applied to one another. The thallus may be attached to the

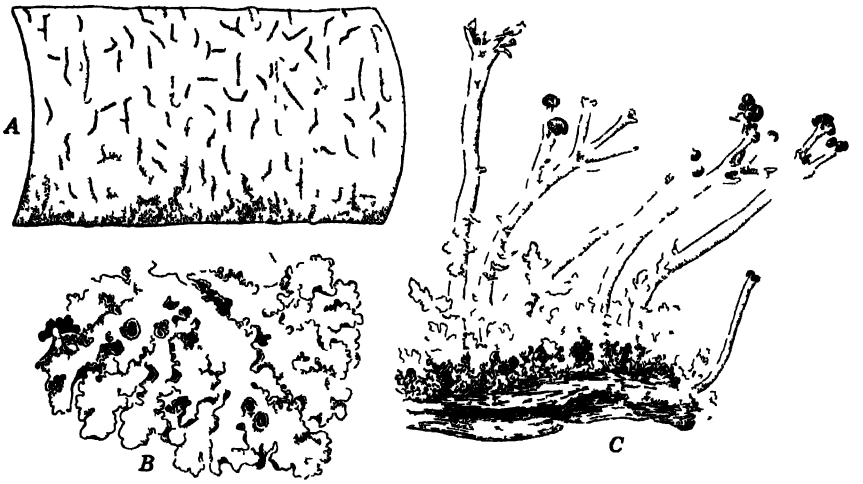


FIG. 293.—*A*, *Graphis scripta* Ach. embedded in the bark of *Alnus*. *B*, *Parmelia flavicans* Tuck. *C*, *Cladonia flabelliformis* (Flk.) Wainio. (*A* × 1½, *B–C*, × ½.)

substratum by a single rhizine growing from the center of the lower face or it may be attached by several rhizines. Still other internally differentiated lichens are *fruticose* and have a much-branched cylindrical to ribbon-like thallus that may be erect or pendant (Fig. 293*C*). Fruticose lichens are attached to the substratum in the basal portion only. The foregoing distinctions between various types of lichens are not absolute. There are intergrading forms all the way from the simplest type of homogeneous crustose lichen to the most highly differentiated foliose thallus.

Structure. Thalli of most foliose lichens are internally differentiated into four tissues (Fig. 294*A*). The uppermost region consists of more or less vertical hyphae that are without intercellular spaces or with the interspaces filled with gelatinous material. This *upper cortex* may or may not be externally limited by an epidermis-like layer of hyphae. *Beneath the upper cortex is the algal layer. It consists of rather loosely*

interwoven hyphae intermingled with algae. At one time the algae were thought to be the reproductive cells of a lichen and were called *gonidia*. This misnomer is still in common use and the algal layer is often called the *gonidial layer*. Beneath the algal layer is a *medulla* composed of very loosely interwoven hyphae. Below this is the *lower cortex*, which consists of compacted hyphae. In some genera the hyphae are more or less perpendicular to the lower face of the thallus; in others they lie

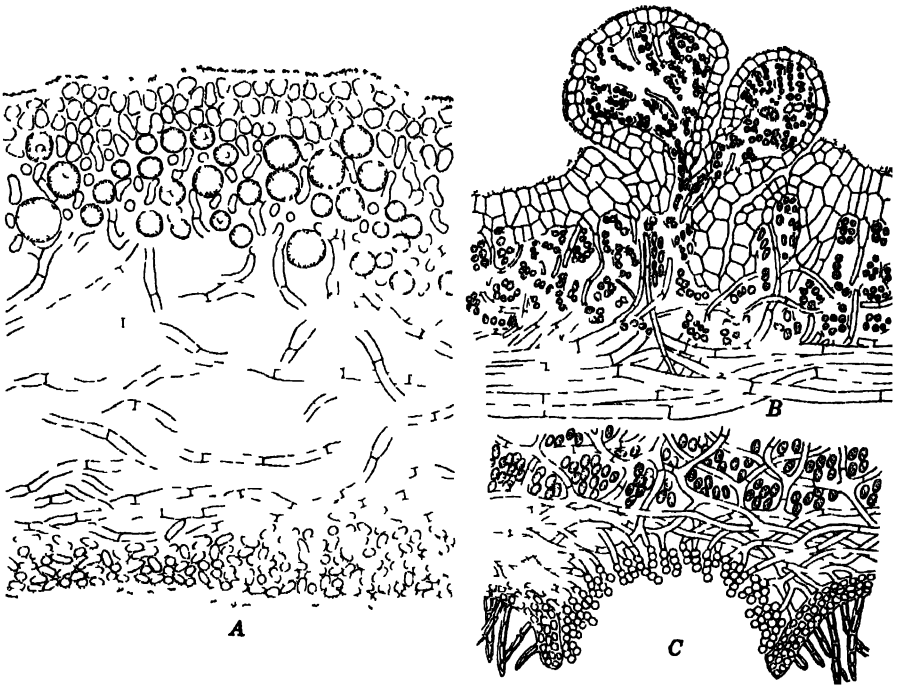


FIG. 294.—*A*, vertical section of a thallus of a species of *Physcia*. *B*, isidia of *Peltigera praetexta* (Flk.) Zopf. *C*, cyphella of a species of *Sticta*. (*B*, *after Darbishire*, 1926, *C*, *after Schneider*, 1897.) (*A*, × 480, *B*, × 150.)

parallel to it. The rhizines grow out from the underside of the lower cortex.

Thalli of fruticose lichens generally have a cortical layer at the outside, an algal layer beneath this, and a central axis of medullary tissue.

In addition to the tissues just enumerated, a thallus may have other vegetative structures. Some foliose and fruticose lichens have a localized differentiation of the cortex into *breathing pores* that facilitate gaseous exchange between interior and exterior of the thallus. Breathing pores of foliose lichens are always developed in the upper cortex. A breathing pore is an area in the cortex where the hyphae are loosely interwoven, and the tissue beneath it is more or less medullary in nature.

A breathing pore may be flush with the surface of the thallus, or it may be a cone-like elevation. The concave circular depressions (*cyphellae*) developed in the lower cortex of a few foliose lichens are also aerating organs (Fig. 294*C*). They are circular breaks in the lower cortex that have been replaced by hyphae which have grown out from the medulla.[1] Cyphellae bear a superficial resemblance to pycnidia because empty, rounded, terminal cells of the hyphae are abstricted in a spore-like manner.

Many lichens have small coralloid outgrowths (*isidia*) from the free surface of the thallus (Fig. 294*B*). Isidia consist of an external cortical layer and an internal algal layer. The alga is the same as that in the thallus. Development of an isidium is generally preceded by a rupturing of the upper cortex, after which medullary hyphae grow into and protrude beyond the wound.[2] The primary function of an isidium seems to be that of increasing the photosynthetic surface of a thallus. Sometimes they become detached from the thallus and serve as vegetative reproductive bodies.

A lichen may also have external or internal gall-like growths (*cephalodia*) in which there are both algal cells and fungal hyphae. An external cephalodium is immediately distinguishable from an isidium by the fact that the cephalodial alga is different from that in the algal layer of the thallus. Cephalodia formed on different individuals of the same species generally contain the same alga.[3] Furthermore, these algae are usually species that enter into the composition of other lichens. In some species the development of cephalodia is due to propagative bodies (*soredia*) of other lichens falling upon young portions of the thallus. Thus, a cephalodium may be looked upon as a small sterile thallus of another lichen and as having no organic connection with the thallus bearing it. Internal cephalodia also contain algae different from those in the algal layer.

Vegetative Multiplication. Continued marginal growth of a lichen may be accompanied by death and decay of the older portions. In these lichens, as in many liverworts, progressive growth and death increase the number of plants. Accidentally several portions of a thallus may develop into a new plant provided they contain both symbionts. This is of frequent occurrence in the "Californian Spanish Moss" (*Ramalina reticulata* Kremp.) where detached portions of the pendant thallus are carried to other trees by winds and there develop into new plants. Reproduction may also be due to a breaking off of outgrowths, especially isidia, from the thallus.

The commonest method of vegetative propagation is by the development of minute bud-like outgrowths (*soredia*) on the upper surface of a thallus. A soredium consists of one or more algal cells enclosed by a few

[1] Schneider, 1897. [2] Darbishire, 1926. [3] Smith, A. L., 1921.

hyphae (Fig. 295*C–D*). They may develop over the entire surface of a thallus or in localized pustule-like areas (*soralia*). Soredia arise in the algal layer in places where there are breaks in the overlying upper cortex. A hypha from the algal layer produces branches that enfold one, two, or more algal cells, and the soredium thus formed is pushed outward by an elongation of the underlying portion of the hypha. The attachment of soredia to the thallus is easily broken, and they are carried in all directions by the wind. If a soredium falls upon a suitable substratum and conditions for growth are favorable, it will immediately develop into a thallus. If conditions are unfavorable for thallus development but not sufficiently unfavorable to check all growth, it will develop other soredia. Sometimes this "soredial dust" forms an extensive coating on trees.

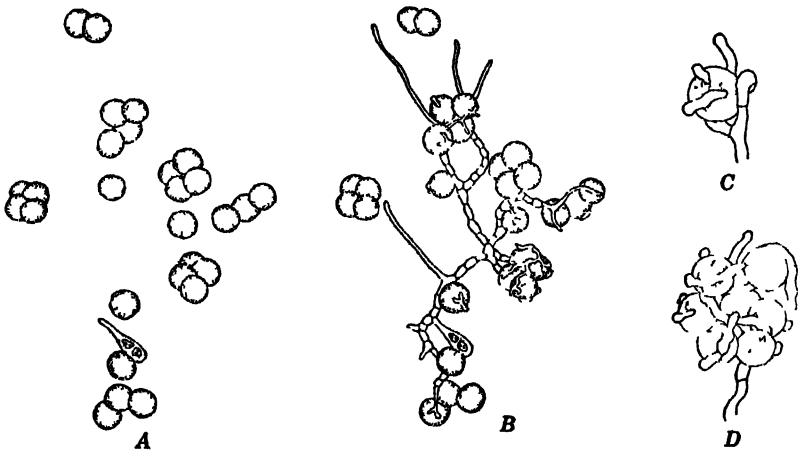


FIG. 295. —*A B*, early stages in synthesis of a lichen thallus *A*, a culture of *Protococcus* (*Trebouxia*?) containing a germinating ascospore of *Physcia parietina* DeNot. *B*, the same culture five days later. *C–D*, soredia of a species of *Parmelia* (*A–B*, *after Bonnier*, 1889.) (*A–B*, × 250, *C–D*, × 650.)

Spore Formation. The fungus of an ascolichen regularly forms spores. When the spore germinates, it sends out hyphal branches that grow in all directions. If one of them comes in contact with a suitable alga (Fig. 295*A–B*), it forms additional branches that enfold the alga.[1] Combined growth of the alga and fungus eventually results in a lichen. If none of the hyphal branches comes in contact with appropriate algae, the hypha dies. However, hyphae of germinating spores may grow indefinitely in artificial cultures when supplied with the proper foods. Under such conditions the mycelium may grow for months and have an external form and internal differentiation of tissues somewhat comparable to that when it grows in association with algae.[2]

Ascolichens may form asexual spores in addition to ascospores. One lichen has been described[1] as producing conidia, but this has been ques-

[1] Bonnier, 1889. [2] Tobler, 1909; Werner, 1926; Killian and Werner, 1924.

tioned.[1] There are also a few well-established cases where the hyphae break up into oidia that may germinate into hyphae.[1] Many lichens produce large numbers of small spore-like bodies within flask-shaped cavities immersed in the thallus (Fig. 296). In certain species the spores are capable of germination, and the hyphae developing from them produce a lichen if they come in contact with appropriate algae.[2] This shows that the flask-shaped cavities of these species are *pycnidia* and that the

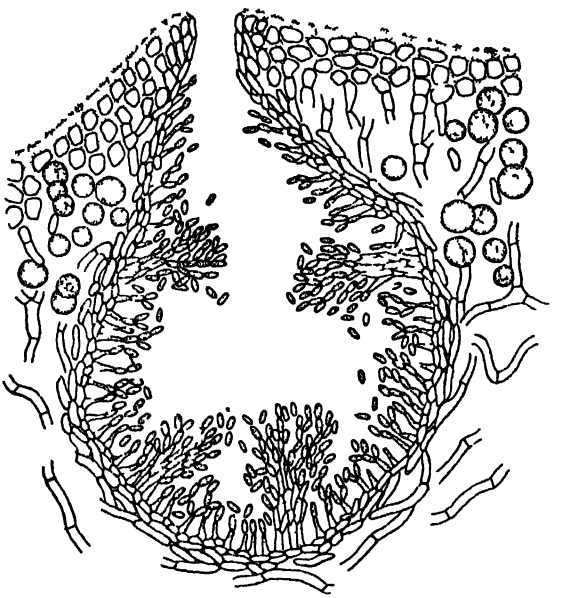


FIG. 296 —Semidiagrammatic vertical section of a pycnidium (spermogonium?) of a species of *Physcia* (× 430)

spore-like bodies within them are *pycnospores*. In the case of certain other species the cavities seem to be *spermogonia* that contain spermatia.

Asci produced by the fungus may be borne in apothecia or perithecia. These may be embedded in the thallus, stand somewhat above it, or be subtended by long stalks. Ascocarp development begins with the differentiation of an ascogonium from hyphae deep in the algal layer. The ascogonia are many-celled and usually have several coils in the lower portion. Ascogonia of most lichens are composed of uninucleate cells, but in certain species the cells are multinucleate.[3] In a large number of species[4] the upper end of an ascogonium is differentiated into a trichogyne whose tip projects beyond the surface of the thallus (Fig. 297*A*). Fertilization in lichens with protruding trichogynes has been described

[1] Smith, A L., 1921 [2] Hedlund, 1895. [3] Moreau and Moreau, 1928, 1932.
[4] Stahl, 1877; Baur, 1898, 1901, 1904; Darbishire, 1900

as being by means of spermatia.[1] The spermatia are produced in flask-shaped spermogonia that lie near the ascogonia. The evidence that the spermatia function as male gametes includes the discovery of spermatia lodged against the sticky protruding tips of trichogynes[1] and the fact that thalli with numerous ascogonia but lacking spermatia rarely produce ascocarps.[2] This is not accepted by all who have studied development of the ascogonia, and it has been held[3] that there is never a fertilization of protruding trichogynes by spermatia. There is at least one species (*Collemodes Bachmannianum* Fink) where the trichogynes never project

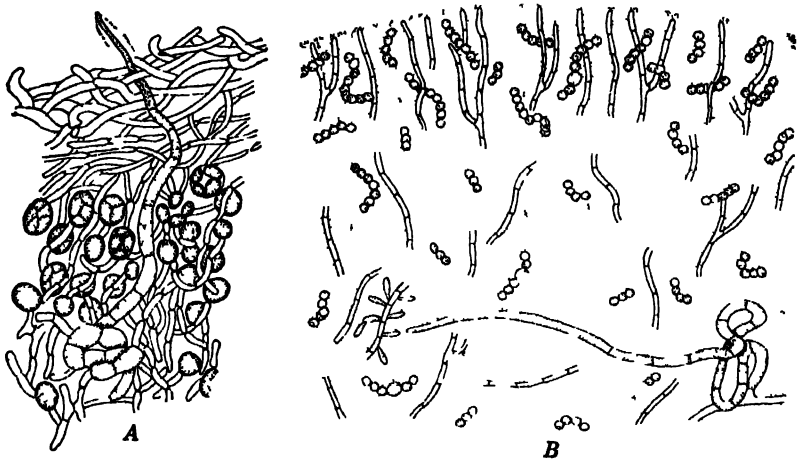


FIG. 297.—*A*, *Anaptychia ciliaris* (L.) Kbr. Ascogonium with an externally protruding trichogyne. *B*, *Collemodes Bachmannianum* Fink. Diagram showing an ascogonium with a trichogyne that remains within the thallus. (*A*, *after Baur*, 1901, *B*, *based upon* Bachmann, 1913.)

beyond the thallus (Fig. 297*B*). Instead, a trichogyne grows more or less horizontally through the thallus until it comes in contact with a cluster of spermatia borne laterally on an internal hypha.[4] The discovery of empty spermatia in contact with such a trichogyne seems to indicate that their protoplasts have migrated into the trichogyne,[5] but an actual migration of male nuclei down the trichogyne has not been seen.

Fertilization is followed by a development of ascogenous hyphae from the basal portion of the ascogonium. In some cases[6] there is a parthenogenetic development of ascogenous hyphae without any preceding formation of ascogonia. The ascogenous hyphae are freely branched and with cells containing one, two, or several nuclei each. Asci are produced at the ends of the ascogenous hyphae. Sometimes[7] the ends are

[1] Stahl, 1877; Baur, 1898, 1901, 1904.
[2] Baur, 1898.
[3] Moreau and Moreau, 1928.
[4] Bachmann, 1912, 1913; Fink, 1918.
[5] Bachmann, 1913.
[6] Darbishire, 1914.
[7] Baur, 1904; Moreau and Moreau, 1928, 1932.

bent in typical croziers, and the binucleate penultimate cell develops into the ascus; sometimes there is a direct development of an ascus from the terminal cell. Ascus development is in the usual manner. When there are two nuclei in a young ascus, the two unite with each other,[1] and the fusion nucleus divides and redivides to form eight daughter nuclei. Eight ascospores are formed by free cell formation, and in most genera each ascospore characteristically divides into two or more cells before liberation.

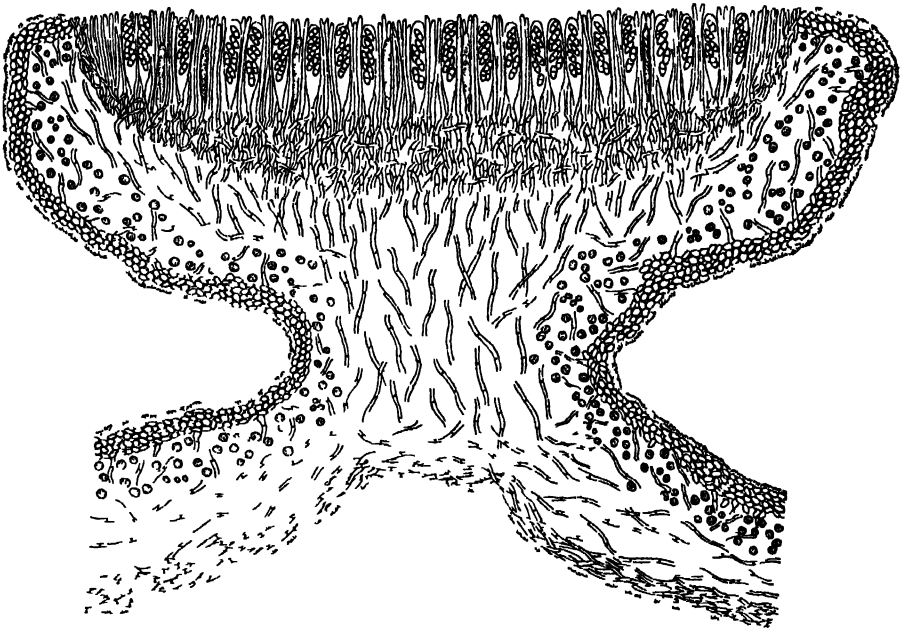


FIG 298.—Semidiagrammatic vertical section of an apothecium of a species of *Physcia*. (× 160)

The ascocarp, whether apothecium or perithecium, is lined with a palisade-like layer of paraphyses (Fig 298). The asci grow vertically upward between the paraphyses but never project beyond them. Ascus development is never simultaneous and in certain lichens an apothecium may continue the production of asci for several years.[2] Discharge of ascospores from perennial apothecia is discontinuous and only takes place during wet weather.[3]

The Ascolichenes are divided into two series: the *Pyrenocarpeae* in which the ascogonium is a perithecium and the *Gymnocarpeae* in which it is an apothecium. The external morphology of the thallus, its internal structure, the nature of the algal symbiont, and the structure of the

[1] Bachmann, 1913; Moreau and Moreau, 1932.

[2] Smith, A. L., 1921 [3] Hiltzer, 1926

ascocarp are characters used in redividing each series into families. Sixteen families are recognized among the Pyrenocarpeae[1] and 35 among the Gynocarpeae.

SUBCLASS 2. BASIDIOLICHENES

There are three genera of lichens in which the fungal component is a basidiomycete. In all of these the fungus is thought to be related to the Thelophoraceae, one of the simpler families of the Agaricales. The algal component is always a member of the Myxophyceae and either nonfilamentous (*Chroococcus*) or filamentous (*Scytonema*). All three genera of basidiolichens are tropical in distribution and found growing upon bare soil, rocks, or trees.



FIG. 299.—*Cora Pavonia* Weber and Mohr. (*After Johow*, 1884.)

The best-known member of the subclass is *Cora Pavonia* Weber and Mohr, a species that is widely distributed in Central and South America on bare soil and on trees. The much-lobed thallus bears a superficial resemblance to a bracket fungus (Fig. 299). When it grows on trees, *C. Pavonia* is laterally attached to the substratum by rhizines. As seen in vertical section, the thallus is differentiated into three layers.[2] The uppermost portion (the *superior layer*) is a loose felt of more or less perpendicular hyphae: beneath this is the *algal layer* in which hyphae run in all directions. The algal component is a species of *Chroococcus*. The *inferior layer* lies below the algal layer and is a rather dense felt of hyphae that run in all directions.

The lower surface of the thallus bears concentrically arranged arcuate outgrowths of more or less perpendicular hyphae. Each outgrowth (*subhymenium*) is radially divided into a number of segments. The lowermost face of each subhymenium bears a palisade-like layer of basidia. Sometimes this is described as consisting of intermingled basidia and unicellular paraphyses, but it is very probable that the so-called paraphyses are immature basidia. Each basidium bears four terminal sterigmata and basidiospores.[3]

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[1] Zahlbruckner, 1926. [2] Mattirolo, 1881; Johow, 1884. [3] Johow, 1884.

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INDEX

Page references in **bold face** refer to pages on which the subject is illustrated or is especially described.

A

Acervulus, **438**, 441, **453**, 457
 nature of, 416
Acetabularia, **125–127**
 mediterranea, **125**, **126**, 127
 Wettsteinii, 125, 126, 127
Acrasieae, **363–364**
 characteristics of, 352, 363
Actinoptychus undulatus, **199**
Aecidiospore, 494, 511
 formation of, **467**, **498**, 499
Aecidium, **498**, 499, 501
Aethalium, **354**, 355
Agar, 325
Agardhiella, **335–336**
 Coulteri, **337**
Agaricales, 469, **474** **479**
 relationships of, **369**
Agaricus campestris, 475
Aglazonia, 242
Agropyron repens, **454**
Akinete, 19, 30, 42, 47, 50, 55, 61, 65, **73**, 81, **117**, 118, 177, 178, 288, **289**, 301, 372, **385**, 432
 germination of, 47, **289**
 liberation of, 61
 nature of, 19, 288
Albuginaceae, **402–405**
Albugo, **402–405**
 candida, 402, **403**, **404**, 405
Algae, 2, 6–8, **12–350**
 bases of classification, 3
 blue-green (*see* Cyanophyta)
 brown (*see* Phaeophyta)
 classes of; 6
 economic uses of, 197, 198, 260, 261, 302, 325
 fossil, 102, **124**, 125, 128, 299
 golden-brown (*see* Chrysophyceae)
 green (*see* Chlorophyta)
 phylogeny of, 6
Algae, red (*see* Rhodophyta)
 thermal, 277
 yellow-green (*see* Xanthophyceae)
Algal layer (lichens), 516
Algin, 221
Alginic acid, 221
Allomyces, 373, **384–386**
 arbuscula, 384, 385
 javanicus, **385**. 386, 372
Alternation of generations, 24, 25, 58, 62, 63, 64, 227–229, 230, 235, 312–314
 antithetic, 314
 origin of, 23
 in Phycomycetae, 373, 386
Amitosis, 130
Amoeba proteus, 163
Amoeboid cells, **163**
Amoeboid movement, 163, 305
Amoeboid stages, 149, 176, 185, 186, 188, 191, **192**, 307, 351, 352, 354, 361, 378 (*See also* Myxamoebae)
Amphora Normani, 211
Amylum star, 130
Anabaena circinalis, **280**, **282**, **284**
 Cycadaea, **291**
 hallensis, **291**
 oscillarioides, **289**
 sphaerica, **289**
Anaptychia ciliaris, **520**
Ancylistaceae, **388–390**
Ancylistales, 374, **388–390**
 relationships of, **369**
Androsporangia, 75, **76**
Androspore, 75
Angiospermae, relationships of, **9**
Anisogamy, 22, 31, **33**, **34**, 35, **57**, 59, 92, 95, **104**, 105, 107, 108, 109, **110**, **113**, 226, 237, **241**, 242, 257, 372, **385**, 386
 nature of, 21, 225, 367
Annuals, 223, 228, 235, 243, 261, 307. 319
Annulus, **475**, 478
Antapical plates, **160**

Antheridial filament, **131**, 132
development of, 132
Antheridial mother cell, **74**
Antheridium, 38, **39**, 48, **52**, 53, **66**, 67, **74**, **76**, 118, **120**, **131**, 132, 226, **239**, 244, **251**, **254**, 255, **265**, 266, 267, 269, 372, **383**, **385**, **387**, 390, **392**, **395**, **399**, 416, **418**, **433**, 434, **443**, 444, 455, 457, **461**
development of, 119, **120**, 245, **246**, **393**, 394, 396, 402, **404**, 460, **461**
initial of, **241**, 245
nature of, 21, 367
Antherozoid, 38, **39**, 48, **53**, **66**, 67, **74**, 119, **131**, 133, **134**, 214, 226, 227, 239, 245, 251, **254**, 255, 266, 267, 271, 372, **387**
development of, 132
liberation of, 74
nature of, 21, 367
Anthocyan, 14
Apical cap, **69**, **71**, 74, **75**, **76**
formation of, **70**
Apical cell, **128**, 129, 131, 145, 223, **236**, **244**, 258, **268**, 306, 319, 325, **326**, 328, **339**, 342, **343**
derivatives from, 129
differentiation of, 273
division of, 235, **268**, 269
Apical plates, **160**
Aplanogamete, 27, **60**, 372, **383**, **393**, **395**, **399**, **404**, **407**, 408, **411**
nature of, 21, 367
Aplanogamy, **210**, **211**
Aplanospore, 19, 26, 42, 45, **46**, 50, 55, 87, 90, **92**, **96**, 98, **115**, 116, 118, 122, **126**, 159, 161, **166**, **178**, 180, 181, 182, 184, 224, 225, 227, 238, 244, 246, 247, **267**, **272**, 371, **380**, 388 391, 432, 469, 471
germination of, 47, **96**, 127, **181**
liberation of, 21
nature of, 19
Apothecium, 424, **443**, 445, 446, 519, **521**
nature of, 418
Appendicular cell, **383**, 384
Appressorium, **495**
Areolae, **201**
Arisaema triphyllum, **121**
Arthrodesmus incus var. *extensus*, **88**
Ascocarp, **418**, 431, **433**, **436**, **439**, 441, **442**, **446**, 447, **448**
Ascocarp, development of, 446, **448**, 449
Ascogenic cell, 462
Ascogenous hyphae, **418**, **419**, 421, 422, 431, **433**, **436**, **439**, 441, **443**, 444, **447**, **449**, 455, **457**, 520
nature of, 418
Ascogonium, **418**, 432, **433**, 434, 435, **436**, 438, **439**, 441, 444, 455, 456, **457**, **461**, **520**
nature of, 416
primary cell of, **461**, 462
Ascolichenes, **514–522**
characteristics of, 514
classification of, 521
structure of, 515–517
vegetative multiplication of, 517–518
Ascomycetae, 366, 367, 368, **415–465**, 466, 511, 514
asexual reproduction of, 415–416
characteristics of, 370, 415
classification of, 424
evolution among, 423
formation of asci, 417–421
nuclear cycle in, 421–422
origin of, 422–423
relationships of, 368, **369**
relationship to Basidiomycetae, 472
sexual reproduction of, 416–417
vegetative structure of, 415
Ascophyllum, 235, 267
Ascospore, 367, 370, 415, **426**, **429**, **430**, 444, **447**, **449**, **451**, **457**, **459**, 460, 511
conjugation of, **430**, 452
ejection of, 421, 437, 440, 442, 447, 450, 455, 458
formation of, **420**, **425**, 429, 437, 442
germination of, **430**, 445, 455, **518**
Ascus, 368, 369, 371, 415, **418**, 421, **433**, **439**, **442**, **447**, **454**, **457**, **459**, 519, **521**
development of, **419**, **420**, **425**, **426**, 427, **428**, **436**, **443**, **448**, **449**, **451**, 462, **472**
homologies with basidium, **472**
Aspergillaceae, 415
Aspergillales, **431–433**
relationships of, **369**
Aspergillus, 415
Asterocystis, 299, **301–302**
ramosa, **301**
smaragdina, **301**
Auriculariales, 473, **490–491**, 493
relationships of, **369**

Autospore, 90, **100**, 101, 166, 195
formation of, **100**, **101**
liberation of, **100**
Auxiliary cell, 310, **329**, **330**, 333, **335**, **337**, **338**, **340**, 341, **345**, **346**
evolution of, 314
position of, 310
Auxiliary-cell filament, **329**, **330**, **332**, **337**, **340**
Auxospore, **208–213**, 214
germination of, 209, 212
Axial field, 201
Azygospore, 81
Azygote, 81

B

Bacillarieae (*see* Bacillariophyceae)
Bacillariophyceae, 156, 168, 183, **195–215**
auxospores of, 208–213
cell division in, 205–208
cell wall of, 198–202
classification of, 214–215
distribution of, 196
fossil, 196–198
locomotion of, 204–205
"microspores" of, 213–214
nature of, 196
protoplasts of, 202–204
statospores of, 208
Bangiales, 300, **301–305**
Bangioideae, 299, **300–305**, 423
characteristics of, 300
Basal cell, 495
Basal pit, 271, **272**
Basidiolichenes, **522**
characteristics of, 514, 522
Basidiomycetae, 366, 367, 368, 370, **466–510**, 511
basidiospores of, 470–471
basidium of, 469–470
characteristics of, 370, 466
classification of, 473
development of, 467–468
diplophase of, 467–469
evolution among, 472–473
haplophase of, 471–472
origin of, 472
relationships of, **369**
Basidiospore, 220, 370, 469, 473, **475**, **479**, **482**, **484**, **486**, **489**, **491**, **492**, 494, **498**, 499, **500**, **501**, 502, **505**, 511, 522
Basidiospore, budding of, **505**
conjugation of, **466**, **506**, 507
dispersal of, 485
ejection of, **469**, 470, 471, 479, 487, 497
formation of, **469**
germination of, 480, **482**, **486**, **489**
secondary, **489**
Basidium, 368, 370, 473, **478**, **484**, **486**, 487, 522
development of, **470**, **472**, **475**, **479**, 481, **482**, 485, **489**, **491**, **500**
homologies with ascus, **472**
origin of, 473
Biddulphia mobiliensis, 213
Smithii, **199**
Blade, **262**
regeneration of, **262**
Blastocladia, 384
Blastocladiaceae, **384–386**
Blastocladiales, 374, **384–386**
relationships of, **369**
Blepharoplast, **16**, 17, 20, 52, 72, 116, 132, 146, **147**, **152**, **157**, 158
Botrydiopsis, **179–180**
arhiza, **180**
Botrydium, 95, 169, 170, 173, **180–182**
granulatum, **173**, **181**
Wallrothii, **181**
Brassica, 360
Breathing pore, 516
Bryophyta, 2, 6, 27
characteristics of, 8
relationships of, **9**, **26**
Bryopsidaceae, **103–105**
Bryopsis, 24, **103–105**
corticulans, 103, **104**, 105
plumosa, 103
Bulbil, 130
Bumilleria sicula, **171**
Bunt, 505

C

Caeoma, 500
development of, **501**
Calcification, 124, 331
Callose, 13, 106, 366
Capillitium, **355**, 483
development of, **355**, 356
Capitulum, **131**
primary, **131**, 132
secondary, **131**

Carotin, 221
Carpogonial filament, 308, 316, **317, 319, 321,** 323, **324, 329, 330, 332, 335,** 336, **337, 340,** 341, **345, 346**
Carpogonium, 295, 299, 300, **303,** 305, 308, **319, 321, 327, 329, 330, 332, 335, 337, 340,** 341, 344, **345**
binucleate, 308, 316, **317**
Carpomitra, **250–252**
cabrerae, **251, 252**
Carposporangium, 310, **317,** 318, **319, 321, 324,** 325, **327, 332, 338, 346**
nature of, 310
Carpospore, 299, 300, **303,** 314, 318, 327
development of, **303, 304,** 305, 309
germination of, 315, 342
liberation of, 320
Carposporophyte, 311, **312, 313,** 314, **317,** 318, **319,** 320, **321, 324, 330,** 333, **335**
nature of, 311
Casts, 124, 128
Caulerpa, 102, **105–107**
clavifera, 107
crassifolia, **106**
cupressoides, **106**
prolifera, **106, 107**
Caulerpaceae, **105–107**
Cell division, 18–19, 41, 51, 57, **70, 71, 80,** 81, 84, **87,** 163, 205, **206**
Cell plate, 53
Cell wall, 221
pores in, 86
structure of, 13, **160,** 169
Celloniella palensis, **184**
Cells, multinucleate (*see* Coenocyte)
Cellulose, 13, 45, 63, 69, 83, 86, 154, 155, 164, 189, 279, 296, 366
Central body, 277, **282**
division of, **282**
nature of, 281
Central filament, 306
Central nodule, 201, **202**
Centrales, 200, 203
auxospores of, **212,** 213
characteristics of, 215
Centriole, **157,** 158
Centrosome, 17, 183, 221
Cephalodium, 517
Ceramiales, **342–348**
Ceratiomyxa, **357–360**
Ceratium, 161
hirundinella, **160**
Chaetoceros, 213
Elmorei, **208**
Chaetophoraceae, 27, 43, **48–50**
Chantransia, **307**
Chamaesiphon, 290
incrustans, **290**
Chamaesiphonales, 277, 289
characteristics of, 292
Chara, **128–135**
crinata, **134**
foetida, **131,** 134
Characeae, **127–135**
Characiaceae, **94–95**
Characium, **94–95**
angustatum, **95**
Charales, 51, **127–135**
Charophyceae, 12, **127–135**
characteristics of, 12, 127
Chilomonas Paramaecium, **152**
Chitin, 14, 63, 69, 279, 366
Chlamydomonadaceae, **29–31,** 40
Chlamydomonas, 15, 17, 18, 19, 26, 28, **29–31,** 32
nasuta, **16,** 17
Chlamydospore, 372, **385,** 386, 388, 411, 416, 469, 502, 503, 504
germination of, **505, 506,** 507
nature of, 372
Chlorarachnion, **176**
reptans, **175,** 176
Chlorochromonas, **174**
minuta, **174**
Chlorochytrium, 90, **93–94**
inclusum, **93**
Lemnae, 93
Chlorococcaceae, **90–92**
Chlorococcales, 26, 27, 50, **89–102,** 166, 174, 373
relationships of, **26**
Chlorococcine tendency, 25, 89
Chlorococcum, **90–91,** 92
humicola, **91**
Chloromeson agile, **172**
Chlorophyceae, 6, **12–127,** 158, 159, 164, 168, 170, 173, 186, 296, 298, 367, 368, 373, 513
alternation of generations in, 23–25
asexual reproduction of, 19–21
cell division in, 18–19
cell structure in, 13–16
characteristics of, 12
classification of, 27

Chlorophyceae, distribution of, 13
evolution among, 26
eyespots of, 16–17
flagella of, 16–17
interrelationships among, **26**
life cycle of, 23–25
sexual reproduction of, 21–22
zygotes of, 22–23
Chlorophyll, 170, 203, 204, 284, 297, 368
Chlorophyll *a*, 221, 222
Chlorophyll *b*, 221, 222
Chlorophyta, 3, 10, **12–142**
characteristics of, 6, 12
relationships of, **9**
Chloroplast, 14–15, 29, **41**, **44**, **46**, 48, **49**, **52**, 55, **57**, 59, 61, 63, **66**, **69**, 79, **83**, 86, **92**, **93**, 95, 100, **101**, 103, 108, 115, 116, 122, **123**, 144, 148
division of, 19
shape of, 15
of zygotes, 22, 23, **82**
Chlorosaccus, **176–177**
fluidus, 176, **177**
Chordaria, 234
Chordariales, **247–250**
relationships of, **229**
Chromatophore, 151, **152**, **153**, 155, 156, 159, 164, **165**, 170, **174**, 176, 177, **178**, 179, **180**, 183, 188, **190**, 191, 192, **194**, **195**, 202, **203**, 221, 223, 231, 245, 297, **301**, **303**, 316
division of, 206
Chromoplasm, 281, 283
Chromulina freiburgensis, **185**
Pascheri, **184**
Chromulineae, **187–188**
Chroococcales, **278**, 287
characteristics of, 292
Chroococcus, 522
turgidus, **278**, **282**
Chrysamoeba, **191–192**
radians, 191, **192**
Chrysocapsales, 164, 186, **192–193**
Chrysochrome, 183
Chrysomonadales, **186–191**
Chrysomonads (*see* Chrysomonadales)
Chrysophyceae, 6, 7, 156, 158, 164, 168, **182–196**, 204, 208
asexual reproduction of, 184–186
cell structure of, 183–184
characteristics of, 182
classification of, 186
Chrysophyceae, distribution of, **182–183**
evolution among, 186
Chrysophyta, 6, 10, **168–219**, **229**
characteristics of, 7, 168
relationships of, **9**, 168
Chrysosphaerales, 186, **195–196**
Chrysotrichales, 186, **193–195**
Chylocladia ovalis, 339
Chytridiales, **374–384**
relationships of, **369**
Chytrids (*see* Chytridiales)
Cilia, 146, 184
Cingulum, 198, 199
Cladochytriaceae, 375, **381–382**
Cladochytrium, **381–382**
replicatum, **382**
Cladonia flabelliformis, **515**
rangifera, 514
Cladophora, **63–65**
glomerata, **64**
Kuetzingianum, **64**
Cladophoraceae, 24, 25, 27, 62, **63–65**, 122
Cladophorales, 27, **62–68**
relationships of, **26**
Clamp cell, **468**
Clamp connections, 466, **469**, 488, 490
formation of, **468**
Classification, 1–10
and alternation of generations, 2
artificial systems, 1
natural systems, 1
Claviceps, **452–455**
purpurea, 452, **453**, **454**, 511
Cleistocarp, 431, 434, 436, 437
development of, **436**
nature of, 418
opening of, 437
Closterium calosporum, **88**
moniliforme, **85**
Cocconeis Pediculus, **200**
placentula var. *klinoraphis*, **211**
var. *lineata*, **212**
Codiaceae, **111–114**
Codium, 21, 24, **111–114**
fragile, 111, **112**, **113**
Coelosphaerium Naegelianum, **278**
Coenobium, 32, **33**, **34**, **36**, **97**, 98, **99**, **101**
formation of, 32, **101**
nature of, 32
Coenocyst, 181

Coenocyte, 14, 26, 55, 62, 64, 65, 89, 91, 94, 95, **97**, 102, 103, 106, 108, 116, 121, **123**, 176, 180, 296, 366, **378**, **383**, 389, 391, 400, 402, 405, 444
division of, 18, 20
nature of, 14
Colaciales, **148–149**
Colacium, **148–149**
calvum, **148**
Coleochaetaceae, 43, **51–54**
Coleochaete, 23, 43, **51–54**
Nitellarum, 53
pulvinata, **52**, 53
scutata, **52**, 53
Collemodes Bachmannianum, **520**
Columella, **406**, **483**, 484
development of, **406**, 407
Complementary chromatic adaptation, 285–286, 298–299
Conceptacle, 266, **270**, 308, 331, **332**, **333**
development of, **268**, 269, **270**
initial of, **268**
Confervales, 373
Conidiophore, 371, 415, **432**, 434, 440, **453**, 456, **457**
development of, **403**, **435**
Conidiosporangium, 371, **397**, 398, 400, **403**, **410**
development of, **403**, **410**
discharge of, 410
germination of, 372, **397**, **401**, **403**, 411
nature of, 371
Conidium, 371, 372, 415, **432**, 434, **438**, 440, **451**, **453**, 455, **457**, **459**, 469, 470, 472, 474, 488, 490, **492**, 502, **506**, 507
conjugation of, **451**, 452
formation of, 432, **435**
primary, **506**
secondary, **506**, 507
Conjugation, gametic, **80**, **84**, **88**, 161, **210**, **211**, **425**, **428**, **430**, 472
of hyphae, 476
lateral, 81
scalariform, **80**, 81, **82**
Conjugation tube, **80**, 161, **428**
Connecting band, 198
Connecting filament, 262, **263**
Consortium, 514
Copromonas, 148
Cora Pavonia, **522**
Coral reefs, 331
Corallinaceae, **331–333**
Corona, **133**
Corona inferior, **125**, 126
Corona superior, **125**, **126**
Cortex, of Charophyceae, 130
development of, **128**, 130
of lichen, 515, **516**
of Phaeophyta, 223, 240, 251, **254**, 262, **268**
development of, **263**
structure of, 264
of Rhodophyta, 316
Corticating branch, 129
Corticating filament, **128**, **133**
initial of, 129
Cortication, 130, 223, 231, **254**
Corticium varians, **468**
Cosmarium, **88**
reniforme, **85**
Cover cell, **347**
Craticular stage, 207
Cryptogamia, 1
nature of, 2
Cryptomonadales, 152
Cryptomonads (*see* Cryptophyceae)
Cryptomonas ovata, **152**
Cryptonemiales, **328–333**
Cryptophyceae, 6, **151–153**
characteristics of, 151
relationships of, 151
Cryptosiphonia, **329–331**
Woodii, **329**, **330**
Cumagloia, 315, **318–320**
Andersonii, **318**, **319**
Cutleria, 239, **240–243**
adspersa, **240**, **242**
multifida, **240**, **241**, **242**
Cutleriales, 221, 226, **239–243**
relationships of, **229**
Cyanophyceae, 277
(*See also* Cyanophyta)
Cyanophyta, 10, **277–294**
cell wall of, 279–281
characteristics of, 8, 277
classification of, 292
heterocysts of, 290–292
locomotion of, 286
occurrence of, 277–278
organization of thallus in, 278–279
pigments of, 284–286
relationships of, **9**
structure of protoplast in, 281–284
vegetative reproduction of, 287–290

Cyclosporeae, **266–273**
characteristics of, 230, 266
Cylindrocapsa, **47–48**, 373
geminella, **47**
involuta, **47**
Cylindrocapsaceae, **47–48**
Cylindrospermum muscicola, **289**
Cymatopleura solea f. *interrupta*, **203**
Cymbella lanceolata, **200**, **210**
Cyphella, **516**, 517
Cyst, **125**, 147, 159, **161**, **163**
(*See also* Statospore)
germination of, **126**, 147, 159, **163**
Cystidia, 488, **489**
Cystocarp, 311
nature of, 311
(*See also* Carposporophyte)
Cystoseira, 267, 268
Cytokinesis, 19
(*See also* Free cell formation; Progressive cleavage)
Cytopharynx, 146, **147**
Cytoplasmic connections, 296
Cytoplasmic streaming, 130, 204, **205**
Cytostome, **145**

D

Dacryomyces, **485–486**, 488
aurantius, **485**
deliquescens, **486**
Dacryomycetales, **485–486**
relationships of, **369**
Dasycladaceae, **124–127**
Delesseria sanguinea, 298
Derbesia, 68, **114–116**
marina, **115**
Derbesiaceae, **114–116**
Dermocarpa pacifica, **290**
Desmarestia, 221, 223, **252–256**
aculeata, **254**
herbacea, **253**, **254**
latissima, 253
Desmarestiales, 226, **252–256**
relationships of, **229**
Desmidiaceae, 27, **84–89**, 184
Desmidium Aptogonum, **85**
Desmids, placoderm, **84–89**
saccoderm, **83–84**
Desmokontae, **153–155**, 162
characteristics of, 153
relationships of, 154
Dextrin, 297
Diatomaceous earth, **197–199**
Diatomin, 203, 204
Diatoms, **196–215**
centric, 199
nature of, 200
characteristics of, 214
"cleaned," 198, 199
dimunition in size, 207
pennate, 200
nature of, 214
(*See also* Bacillariophyceae)
Dictyosiphon, **258–259**
foeniculaceus, **258**
Macounii, **258**
Dictyosiphonaceae, **258–259**
Dictyosiphonales, 225, **257–259**
relationships of, **229**
Dictyostelium, **363–364**
Dictyota, 220, 244, 245
Dictyotales, 220, 221, 226, **243–247**
relationships of, **229**
Didymium, **353**
Dinamoebidium, **163–164**
varians, **163**
Dinastridium sexangulare, **166**
Dinobryon, **189–191**
calyciforme, **190**
divergens, **190**
sertularia, **190**
stipitatum, **190**
Tabellariae, **190**
Dinocapsales, **164**
Dinococcales, **165–166**
Dinoclonium, 164
Conradi, **165**
Dinoflagellates (*see* Dinophyceae)
Dinophyceae, 6, **155–166**
cell walls of, 155–156
characteristics of, 155
classification of, 158
structure of protoplast, 156–158
Dinophysidales, **162–163**
Dinophysis acuta, **162**
Dinothrix, 164
paradoxa, **165**
Dinotrichales, **164–165**
Dioecism, 107, 111
Diplanetism, 392, 398
Diplohaplont, **24**, 25, 56, 62
Diplonema, 228, 259
Diplont, **24**

Diplophase, 487, 490, 493, 497, 498, 502
formation of, **466, 467, 471, 504**
nature of, 466
spore formation by, 468, 469
Dipodascus, 415, 417, 423, **425–427**
albidus, 425, **426**
Discomycetae, 424, 431
Dothidiales, 431, **458–460**
relationships of, **369**

E

Ectocarpaceae, **231–235**
Ectocarpales, 225, **230–235**, 247
relationships of, **229**
Ectocarpus, 223, **231–234**, 237, 248, 259
acutus, **232**
cylindricus, **232**
siliculosus, 228, **232**, 233, 234
Egg, **39, 47**, 48, **66**, 67, 132, 214, 226, 227, **239, 246, 254**, 255, 266, 267, 271, 372, **387, 399**
formation of, **393, 404**
nature of, 21, 367
Elaioplast, 203
Empusa, 408, **409–411**
fumosa, **411**
muscae, 409, **410**, 411
Endogelatin, 271
Endomycetales, **424–430**
relationships of, **369**
Endoperidium, 481, **482**
Endosphaeraceae, **92–94**
Endospore, **290**
Endospore layer, 40
Endosporeae, **353–357**
characteristics of, 353
Endosporine tendency, 25
Enteromorpha, 56
compressa, 298
Entomophthora, 408, **409**, 411
fumosa, 411
Entomophthorales, **408–411**
relationships of, **369**
Entosiphon sulcatum, **145**
Epibasidium, **486, 489, 491, 492**, 497, **498**, 499, **500, 501**, 502, 504, **505, 506**, 507
nature of, 469
Epichrysis, **195–196**
paludosa, **195**
Epidermis, 240, 262, 264
Epilithon membranaceum, 331
Epiplasm, **420**
Epitheca, of diatoms, 198, **199, 200, 206**, 209
formation of, **206**
of dinoflagellates, **160**, 161, **162**
division of, **160**, 161
Epithecium, **439**, 440
Eremascus, 416, 417, 423, **424–425**, 427
fertilis, 424, **425, 426**
Ergot, 452
Ergotism, 452, 453
Erysiphaceae, 415
Erysiphales, **434–437**
relationships of, **369**
Erysiphe, 415, 416, **434–437**
aggregata, **420, 436**
cichoraceum, **435**
graminis, 437
Euascomycetae, 417, **431–462**, 473
characteristics of, 424, 431
Euastrum affine, **85**
Eubasidii, 469, **473–492**
characteristics of, 473
Eucapsis alpina, **278**
Eudorina, 32, **34–36**
elegans, **34**
unicocca, **34**
Euglena, 144, 148
intermedia, **145**
sanguinea, 144
Euglenales, **144–148**
asexual reproduction of, 147
cell shape of, 144
cell structure in, 144–147
classification of, 148
sexual reproduction of, 147–148
Euglenocapsales, **148–149**
Euglenoids (*see* Euglenales)
Euglenophyta, **143–150**
characteristics of, 7, 143
relationships of, **9**
Eumycetae, **366–512**
characteristics of, 8, 366
classification of, 370
evolution among, 368–370
origin of, 368
relationships of, **9**
sexual reproduction of, 368–376
Eunotia diodon, **203**
Exit papilla, **107**
Exit tube, **378, 382, 383, 389**

Exoascales, **450–452**
relationships of, **369**
Exoascus, 450
Exobasidium, **474–475**
Vaccinii, 474
Exochite, 271, **272**
Exoperidium, 481, **482**
Exospore, 40, 290
Exosporeae, **357–360**
characteristics of, 353, 357
Exuviaella, **154–155**
marina, **154**
Eyespot, **17**, 35, **44**, **64**, 157, 179

F

Fairy ring, 479
Fats, 16, 204, 222, 429
Fertile layer, 269, **270**
Fertilization, **39**, **47**, 48, 53, **66**, 68, **75**, 77, 119
(*See also* Oogamy)
Fertilization tube, 390, **393**, 394, **395**, 396, **404**
Filament, 279, **280**
Flagella, **16**, **29**, 35, 37, 72, **152**, **174**
dimorphic, 154, **157**, **159**, 161, **171**
structure of, 17, 146, 157, 171, 184
Flagellata, 4, 168
Florideae, **305–348**, 423
alternation of generations in, 312 314
carpospore of, 309–311
germination of, 311–312
characteristics of, 300, 305, 311, 315
classification of, 314
evolution among, 314
gametic union of, 309
reproduction of gametophyte in, 307–309
vegetative structure of, 306–307
Floridean starch, 297
Foot cell, **495**
Fountain-type thalli, 306
Fragilaria virescens, **201**
Free cell formation, 417, **420**, 421, 423, **437**
Fruiting pillar, **358**
Frustule, 198, **199**, **200**, **208**
girdle view of, 198, **199**
valve view of, 198, **199**
Fucaceae, 220, **266–273**
Fucales, 221, 223, 226, 227, 228, 260, **266–273**
oogamy of, 226
relationships of, **229**
Fucosan granules, 221
Fucoxanthin, 7, 220, 222
chemical composition of, 222
Fucoxanthin *a*, 222
Fucoxanthin *b*, 222
Fucus, 235, 267, 268, 273
Fuligo septica, **354**
Fungi, 2, 8, **351–512**
bases of classification of, 3, 4
fossil, 368
origin of, 4, 6
perfect stage, 511
Fungi imperfecti, **511–512**
characteristics of, 370, 511
Fungus cellulose, 366
Funnel cleft, **202**
Fusicladium dendriticum, 456, 511

G

Gaidukov phenomenon, 285
Gametangium, 55, **104**, 108, **110**, **125**, 225, 226, 232, 237, 244, **249**, 250, **257**, 259, 361, **407**, 408, 417, **425**, **426**
development of, 108, 109, **110**, 111
female, 237, 426, **427**
development of, **241**
male, 237, 426, **427**
development of, **241**
(*See also* Antheridium; Oogonium)
Gametic union (*see* Anisogamy; Isogamy; Oogamy)
Gametophyte, 134, 222, 223, 224, 226, **227**, 233, 234, 235, 237, **238**, **240**, 243, **248**, **249**, **251**, **257**, 259, 307, **312**, **313**, **317**, **318**, **322**, **329**, 331, 336, **337**
of Basidiomycetae, 466
female, **244**, **254**, 255, **265**, 266
male, **254**, 255, **265**, 266
Gas vacuole, 283
Gasteromycetae, 479
Gasteromycetes, 467, 469, 473
Gastroclonium, **339–342**
Coulteri, **339**, **341**, 342
ovale, 339, **340**
Gelidiales, 314, **325–328**
Gelidium, **325–328**
capillaceum, **326**
cartilagineum, **326**, **327**

Gemma, 392
Germ pore, **495**
Gigartinales, **334–338**
Gill (*see* Lamella)
Girdle, 155, **162**
Gleba, 481, **482, 483, 484**
 development of, 481, **482**
Glenodinium uliginosum, **161**
Globule, 130, **131, 133**
 development of, 130, **131**
 interpretation of, 132
Gloeodinium montanum, **164**
Gloeothece linearis, **278**
Glycogen, 183, 283, 366, 368, 429
Gonapodya, 386
Gonidial layer, 516
Gonidium, 516
Gonimoblast filament, 309, **317**, 318, **319, 324, 327, 330, 335**, 337, **338, 340**, 422
 initial of, **329, 338**, 341, **346**
Gruphis scripta, **515**
Grinnellia, **307**
Gullet, **145**, 146, **152**, 153
Gymnocarpae, 521
 characteristics of, 521
Gymnoconia Peckiana, 500, 502
Gymnodiniales, **158–159**
Gymnodinium abbreviatum, **159**
Gymnogongrus Griffithsiae, 314
Gymnospermae, relationships of, **9**

H

H-piece, 45, **46**, 169, **170**, 177, 178
Haematochrome, 15, 39, 55, 144
 function of, 55
Halicystaceae, **107–111**
Halicystis, **108–111**
 ovalis, 108, **109, 110**
Handle cell, **131**
Haplont, **24**, 43
Haplophase, 467, **471**, 483, **486**, 490, 493, 498, 502, 503
 nature of, 466
Haplospora, **237–239**
 globosa, 237, **238, 239**
Haplostichineae, **247–256**
 characteristics of, 247
 validity of, 256
Hapteres, 261, **262**
Haustorium, 400, 402, 434, **435**, 495
Helotism, 513
Helvella, **448–450**
 crispa, **448**, 449
 elastica, **448**
Helvellales, 431, **448–450**
 relationships of, **369**
Hemibasidii, 469, 470, 491, **493–507**
 characteristics of, 473, 493
Hemicellulose, 70, 281
Hemidinium nasutum, **161**
Hesperophycus, 267, 268
 Harveyanus, **272**
Heterocapsales, 164, 174, **176–177**
Heterochloridales, 173, **174**
Heterococcales, 174, **179–180**
Heterocyst, 288, 290–292
 development of, 290
 function of, 291
 germination of, **291**
Heterogamy, 372
Heterogeneratae, **227, 247–266**
 characteristics of, 230, 247
Heterokontae (*see* Xanthophyceae)
Heterosiphonales, 174, **180–182**
Heterospory, 267
Heterothallism, 31, 35, 38, 42, 53, 56, 65, 74, 76, 78, 97, 118, 225, 226, 240, 245, 304, 308, 322, 331, 335, 336, 344, 372, 407, 408, 416, 432, 438, 452, 468, 472, 497, 502, 504
 nature of, 22
Heterotrichales, 174, **177–179**
Hilum, 470
Hirneola, **490–491**
 auricula-judae, **490, 491**
Holdfast, 58, 59, 69, 242, 243
Homothallism, 31, 35, 38, 53, 74, 97, 118, 182, 225, 304, 308, 316, 320, 322, 372, 416, 428
 nature of, 22
Hormogonales, **280**
 characteristics of, 292
Hormogone, 286, **287**, 288
Hormospore, **287**, 288
Hydrodictyaceae, 27, 90, **97–100**
Hydrodictyon, **16**
Hydrurus, **192–193**
 foetidus, 192, **193**
Hymenium, 466, **447, 449, 478, 486, 491, 492**
 nature of, 469
 primordium of, 477
Hymenomycetae, 474

Hymenomycetes, 467, 469, 473
Hypha, of fungi, 366
conjugation of, **467, 471**
of Phaeophyta, 262, **263**
development of, **263**
trumpet, **263**
Hyphal body, 409, **411**
multiplication of, 409
Hypnospore, 19, 30, 42, 98, 118, 180, 182
germination of, 118
Hypobasidium, **486**, 487, **489, 491, 492,** 497, **498**, 499, **500, 501, 506**
nature of, 469
Hypocreales, 431, **452–455**
relationships of, **369**
Hypothallus, 355, 357, **358**
Hypotheca of diatoms, 198, **199, 200, 206**, 209
formation of, **206**
Hypotheca of dinoflagellates, **160, 162**
division of, **160**, 161
Hypothecium, **439**
Hysteriales, 431, **437–440**
relationships of, **369**

I

Impressions, 124
Inner fissure, **202**
Intercalary plates, **160**
Internode, **128**, 129, **133, 134**, 135
development of, 129
initial of, **128**
Inversion, 32, 37, **38**
Iodine, sources of, 260
Iridaea, **334–335**
cordata, **334, 335**
Isidium, **516**, 517
Isochrysidineae, **188–189**
Isogamy, 22, **31**, 50, 59, 65, **80, 88**, 91, 92, **94, 96**, 99, 107, 124, **126**, 127, **173**, 178, 182, 191, 225, 226, 230, **232**, 237, 259, **356**, 357, **359**, 360, 361, 372, **377, 379, 380**, 381, 382, **407**, 408, **411, 426**
nature of, 21, 225, 367
Isogeneratae, **227, 230–247**
characteristics of, 230
Isthmia enervis, **199**
nervosa, **201**
Isthmus, **85**
Ithyphallus, **483–485**
impudicans, **483, 484**

J

Jacket cell, primary, **461**, 462

K

Kelps, 222, 223
(*See also* Laminariales)
Kombu, 260–261
Kunkelia nitens, **500–502**

L

Laboulbeniales, **460–462**
relationships of, **369**
Lagenidium, **388–390**
Rabenhorstii, **389**
Lamella, **477, 478**
Laminaria, **261–266**
Andersonii, **262, 263**
digitata, **263**
ephemera, 261
Farlowii, **262**
flexicaulis, **265**
saccharina, 265
Laminariales, 220, 221, 223, 226, 255, **259–266**
relationships of, **229**
Laminarin, 7, 222
nature of, 222
"Leaf" of Charales, **128**
development of, **128**, 129
Leathesia, 220, 223, 228, **249–250**
amplissima, **249**
difformis, **249**
Leptomitaceae, **394–396**
Leptomitales, 395
Leucosin, 170, 176, 183, 188, 190, 191, 194, 204
Liagora, **320–321**
pinnata, **320**
tetrasporifera, 310, 313, **321**
viscida, **321**
Lichens, 366, 415, **513–523**
algae of, 91, 513
classification of, 514
crustose, **515**
distribution of, 514
foliose, **515**

Lichens, fruticose, **515**, 516
growth on rocks, 514
nature of, 513
spore formation by, 518–521
synthesis of, **518**
Life cycles, of Chlorophyta, 23–25
of Florideae, **312**, **313**
of Phaeophyta, **227–229**, 233
Lime, deposition of, 127, 128
Lithophyllum, 108
Lithothamnion, 108, **331–333**
mediocre, **331**, **333**
membranaceum, 331
Locomotion, of desmids, 86
of diatoms, 204–205
of Cyanophyta, 286
Lomentaria ovalis, 339
Lophodermium, **437–440**
hysterioides, 437, 439
pinastri, 437, **438**, **439**
Lorica, 144, 147, 175, 183, 189, **190**, 191
Lycoperdales, 469, **479–485**
relationships of, **369**
Lycoperdon, **480–483**, 484
gemmatum, **482**
pyriforme, **480**
Lycopsida, 5
Lyngbya Birgei, **287**

M

Macrocystis pyrifera, 259, **260**
Macrosporangium, 227, 229, **272**
development of, 267, **269**, **270**, 271
Macrospore, 227, **272**
Mallomonas, **187–188**
caudata var. *macrolepsis*, **187**
coronata, **184**
Mannitol, 222
Manubrium, **131**, 132
Medulla, of Phaeophyta, 223, 251, 262, **268**
of lichens, **516**
Meiosis, 23, 31, 39, 45, 53, 64, 77, 78, 83, 84, 89, 93, 105, 112, 120, 124, 126, 133, 209, **210**, **211**, 213, 224, 227, 231, 233, 237, 243, 246, 264, 265, **269**, 309, 311, 314, 317, 320, 324, **328**, 351, 357, 359, 362, 367, 368, **370**, 373, 379, 388, 402, 421, 422, **425**, 430, 436, 451, 470, 499
Melanconiales, 512
characteristics of, 512
Melosira, 212, 213
varians, **212**
Merismopedia elegans, **278**
Meristem, 223, 261
Mesochite, 271, **272**
Mesogelatin, 271, **272**
Mesospore, 40
Mesotaeniaceae, **83–84**
Mesotaenium Grèvii var. *breve*, **83**
Micrasterias apiculata, **85**
Microcoleus vaginatus, **280**
Microcystis aeruginosa, **278**
Microspora, **45–47**
Willeana, **46**
Microsporaceae, **45–47**
Microsporangium, 227, 229, 267, **270**
development of, 269
Microspore, 213, 227, 267, **272**
formation of, **213**
liberation of, 213, 272
Moniliales, 512
characteristics of, 512
Monoaxial thalli, 306, **307**, **326**
Monoblepharidaceae, **386–388**
Monoblepharidales, 374, **386–388**
relationships of, **369**
Monoblepharis, **386–388**
macrandra, **387**
polymorpha, **387**
Monoecism, 111
Monosiphonous thalli, 237, **238**
Monosporangium, 225, **238**, **239**, 307, 314, 322, **323**
Monospore, 225, 238, **239**, 299, 300, 306, 307, 322, 389
Mucilage canal, **262**, 264
Mucorales, 372, **405–408**
relationships of, **369**
Multiaxial thalli, 306, 315, **318**, 322, **385**, 336, **339**
Musca domestica, 460
Mycelia Sterila, 511
characteristics of, 512
Mycelium, 8, 366, 371, 384, **385**, **387**, **389**
Mycetozoa, 351
Mycorhiza, 446
Myrionema, **248**, 250
strangulans, 220, **248**
Myxamoebae, 351, 361, **363**, 364
division of, **363**

Myxomycetae, 351, **352–360**
characteristics of, 352
Myxophyceae, 6, 156, 277, 297, 299, 300, 513
(*See also* Cyanophyta)
Myxophyta, 351
Myxothallophyta, **351–365**, 366
characteristics of, 8, 351
relationships of, **9**

N

Nannandrium, **76**
development of, **76**
Nannocyte, 290
Navicula radiosa, **203**
rhyncocephala, **200**
Nemalion, **315–318**, 319, 320
multifidum, **317**
Nemalionales, 309, 314, **315–325**
Nematheeium, 308, 331, **332**
Nereocystis, 223, 264
Luetkeana, **260**, 302
Netrium, 84
digitus, **83**, **84**
Neuromotor apparatus, **16**, 20, 37, 50, **147**, **152**, **157**, 158, 184, 188
division of, **16**, 17, **147**, **157**, 158
Neurospora, 422
Neutral spore, of Phaeophyta, 228
of Rhodophyta, 299, 300, **301**, 304
Node, **128**, 129, **133**, **134**, 135
development of, 129
initial of, **128**, 129
Nodularia spumigena, **289**
Nostoc commune, **291**
muscorum, **289**
Nostocaceae, 286
Nostochopsis lobatus, **280**
Nucleic acids, 204
Nucleus, 146, **152**, 153, **154**, 155, **157**
division of, 14, 64, 146, 147, **157**, 183, 192, 204, 221, 304
structure of, 183, 204, 221, 297
Nucule, 130, **133**
development of, 132, **133**
Nurse cell, 310, **323**, 324, **329**, **330**
Nurse tissue, 310, **327**, 337, **338**

O

Ocellus, 157
Ochromonadineae, **189–191**
Ochromonas crenata, **185**
stellaris, **184**
Oedogoniaceae, 27, **68–79**
Oedogoniales, 23, 27, **68–78**
gynandrosporous, 75
idioandrosporous, 76
macrandrous, 74, **75**
nannandrous, 74, 75, **76**
evolution of, **77**
relationships of, **26**
Oedogonium, 18, 23, 24, **68–79**
concatenatum, **76**
crassum, **69**, **70**, **75**
Oidia, 272, 392, 416, 444, 469, **471**, **486**, 487, 492
Oil, 116, 156, 170, 203, 283
(*See also* Fats)
Olpidiaceae, 375, **377–379**
Olpidiopsis, 382, **383–384**
Saprolegniae, **383**
vexans, **383**
Olpidium, 375, **377–379**
Viciae, **378**, **379**
Ooblast, 310, **329**, **330**, **332**
Oocystaceae, 90, **100–101**
Oogamy, 22, 38, **39**, **47**, **48**, **52**, 53, **66**, 73, **75**, **76**, 118, **120**, 133, **134**, 226, 230, **239**, **246**, 266, 271, **272**, 369, 372, **383**, **387**, 388, **389**, 390, **393**, **395**, 396
nature of, 21, 225, 367
Oogonial cell, primary, **246**
Oogonial mother cell, in Charales, 132
in Oedogoniales, 74, **76**
Oogonium, **47**, 48, **52**, 53, **66**, 67, **75**, **76**, 118, **120**, 132, **133**, **239**, 244, **246**, **251**, **254**, 255, **265**, 266, 267, 372, **383**, **385**, **387**, 390, **392**, **395**, **399**, **443**
development of, 74, **75**, **76**, 119, **120**, **393**, 396, 398, 402, **404**
nature of, 21, 367
Oomycetae, 374
Oomycetes, 373, 374
Ophiocytium, 169
Oscillatoria formosa, **280**
limosa, **280**
princeps, **282**
Oscillatoriaceae, 286
Ostiole, 269, **270**, 337, **338**, **454**, **457**, 458, 497
Outer fissure, **202**
Oxyrrhis marina, **157**

P

Palaeodasycladus mediterraneus, **124**
Palmella stage, **29**, 30, 35, 40, 43, 47, 91, 147, 149, 153, 164, 188, 189, **194**
Pandorina, 21, 32, **33–34**
morum, **33**
Paradesmose, **16**, 17
Paramylum, 145
Paraphyses, **246**, **251**, 256, **257**, 269, **270**, **418**, **439**, **521**
Parasporangium, 312, **341**, 342
Paraspore, 299, 306, **341**
formation of, 342
nature of, 312
Parmelia, **518**
flavicans, **515**
Parthenogenesis, 45, 50, 59, 65, 77, 93, **96**, **212**, 226, 227, 228, 233, 234, 252, 259, 310, 381, 417, 425, **426**, 428, 429
nature of, 22
Parthenospore, 22, 77, 81, 87, 394, 411
Pectic sheath, 13
Pectose, 13, 55, 63, 69, 79, 83, 86, 169, 366
Pediastrum, 20, **97–100**
Boryanum, **97**, **99**
Pedicel cell, **131**, 132, **133**
Peltigera praetexta, **516**
Pelvetia, 223, 267, **268–273**
canaliculatus, 271
fastigiata, **268**, **270**, 271, **272**
Penicillium, **431–433**, 511
vermiculatum, 432, **433**
Pennales, 200, 203
auxospores of, 208–212
characteristics of, 215
Perennials, 223, 228, 235, 243, 245, 261, 269, 307, 325, 334
Pericarp, 311, 323, **324**, **345**, **346**
Pericentral cell, **326**, **343**, 344
fertile, 344
Peridiniales, **159–161**, 162
Peridinin, 156
Peridinium wisconsinense, **160**
Peridium, 352, **355**, **418**, 431, 435, 450, **457**, 481, **482**, **498**, 499
development of, **436**
Peripheral cell, **347**
Periplasm, **395**, 396, **399**, 402, **404**
Perisporales, 434
Perithecium, 424, 437, **454**, 455, **457**, **459**, **461**, 519, 521
Perithecium, development of, 456, **457**, **459**
initial cell of, **461**, 462
nature of, 418
Peronosporaceae, **400–402**
Peronosporales, 374, 396, 397, **399–405**
relationships of, **369**
Pezizales, 431, **443–445**
relationships of, **369**
Pfitzer's Law, 206, **207**
Phacidiales, 431, **440–442**
relationships of, **369**
Phaeophyceae, 6, 156, 168, 296, 298
Phaeophyta, 3, 10, **220–276**, 367
alternation of generations in, 227–229
asexual reproduction of, 224–225
cell structure of, 221
characteristics of, 7, 220
classification of, 230
distribution of, 220–221
evolution among, 229–230
origin of, 229
pigments of, 221–222
relationships of, **9**
reserve foods of, 222
sexual reproduction of, 225–227
thallus structure in, 222–224
Phaeoplax marinus, **153**
Phaeothamnion, **194–195**
Borzianum, **194**
confervicola, **194**
Pharyngeal rods, **145**, 146
Phialopore, 32, 37, **38**
Photosensitive substance, **17**
Phragmidium speciosum, **467**
Phragmoplast, 18
Phycochrysin, 183
Phycocyanin, 8, 156, 277, 284, 285, 295, 297, 300, 303
Phycoerythrin, 8, 277, 284, 295, 297, 300
function of, 298
Phycomycetae, 366, 367, 368, **371–414**, 466, 511
asexual reproduction of, 371–372
characteristics of, 370, 371
classification of, 374
evolution among, 373–374
life cycles of, 373
origin of, 373–374
relationships of, **369**, 422
sexual reproduction of, 372–373
Phycopyrrin, 156

Phyllophora Brodiaei, 313, 314
Phyllosiphon, **121–122**
Arisari, **121**
Phyllosiphonaceae, **121–122**
Phyllospadix, 302
Physarum, **355**
alpinum, **354**
polycephalum, **356**
Physcia, **516**, **519**, **521**
parietina, **518**
Phytomyxinae, 352, **360–364**
characteristics of, 352, 360
Pileus, **475**, **477**, **483**
Pinnularia, 201, **202**, **205**
Pinnule, 103
Placental cell, **317**, 318, **332**, 333, 342, **346**
Plakea, 32, 33, 35, 37, **38**
Plasmodial stage, 149
Plasmodiocarp, **354**, 355
Plasmodiophora, **360–364**
Brassicae, 360, **361**, **362**
Plasmodiophoraceae, 352, **360–364**
Plasmodiophorales, **360–364**
Plasmodium, **175**, 176, 186, 351, 352, **353**, 354, 357, 361, **362**
Plasmopara, **400–402**
Halstedii, 400
viticola, 400, **401**, 402
Plectascales, 431
Plectomycetae, 424, 431
Plethysmothallus, 228, 250
Pleurococcus, 50
Plowrightia, **458–460**
morbosa, **458**, **459**
Polar cleft, **202**
Polar nodule, of diatoms, 201, **202**
of Myxophyceae, 291
Polyeder, **99**, 100
germination of, **99**
Polysiphonia, **342–348**
flexicaulis, **343**, **345**, **346**
lanosa, 344
nigrescens, 344
Polysiphonous thalli, 235, **236**, 237, **238**, **343**
Polyspore, **306**, 307
Polystichineae, **256–266**
characteristics of, 247, 256
Pore, **201**
Pore plate, 162
Poroid, **201**
Porphyra, 60, 61, 299, 300, **302–305**
naiadum, **302**
Nereocystis, 302
perforata, **303**, 304
tenera, 303, 304
Porphyrosiphon Notarisii, **280**
Postcingular plates, **160**
Postelsia, 234
palmaeformis, 260, **261**
Potassium, sources of, 260
Prasiola, **60–62**, 300, 302
meridionalis, **62**
mexicana, **62**
Precingular plates, **160**
Prelamellar chamber, **477**
Progametangium, **407**
Progressive cleavage, 20, 64, **66**, 67, 89, 91, 94, **95**, 96, **97**, 109, 112, 115, **355**, **358**, 375, 380, 382, 385, 391, 398, **406**, 407
Proliferation, 96
Promycelium, 470
Propagulum, 224, 235, **236**
development of, **236**
Protoascomycetae, 417, 421, **424–430**, 431, 452, 473
characteristics of, 424
Protococcaceae, **50–51**
Protococcus, 42, **50–51**, **518**
viridis, **51**
Protonema, 110, 130, 228, 315, 318
initial of, **134**
primary, **134**, 135
secondary, **134**, 135
Protosiphon, 26, **95–97**
botryoides, 95, **96**
Protosiphonaceae, **95–97**
Protozoa, relationship to fungi, 351, **368**, **369**, 373
Psalliota, **475–479**
campestris, 475, **476–479**
Pseudobryopsis, 103
Pseudocilia, **41**
Pseudoplasmodium, 351, **363**, **364**
Pseudopodium, 156, 163, 191
Pseudoraphe, **200**
nature of, 201
Pseudovacuole, **284**, **293**
structure of, **283**
Psilophyta, 5

Psilopsida, 5
Pteridophyta, 2, 6
 bases of classification of, 5
 characteristics of, 9
 interrelationships among, 5
 relationships of, **9**
 validity of, 4–5
Pteropsida, 5
Pterygophora, 223
Puccinia graminis, **494–499**, 501
 malvacearum, **499–500**
Puffing, 450
Pulsule, 157
Punctariales, 221, 225, **256–257**
 relationships of, **229**
Pycnidium, 438, 441, **519**
 nature of, 416
Pycnium, 497
Pycnospore, 416, **519**
Pylaiella, **234–235**
 Gardneri, **234**
 littoralis, 234, 235
Pyrenocarpeae, 521
 characteristics of, 521
Pyrenoid, 15, **16**, **29**, **41**, **44**, 48, **49**, **52**, **57**, 59, **69**, 86, **92**, **101**, 103, 108, **123**, 144, 148, 153, 179, 180, 183, 192, 203, **303**, 316
 division of, 16, **87**
 naked, 297
Pyrenomycetae, 424, 431
Pyronema, 415, 416, 418, **443–445**
 confluens, 416, **419**, **443**, 444
Pyrrophyta, 6, 10, **151–167**
 characteristics of, 7, 151
 relationships of, **9**
Pythiaceae, **396–399**
Pythium, **397–399**
 aphanidermatium, **397**, 398, **399**
 intermedium, **397**, **399**

R

Ramalina reticulata, 514, 517
Ranunculus aquatilis, 177
Raphe, **200**
 nature of, 201
 structure of, **202**
Receptacle, 266, 269
Reduction division (*see* Meiosis)
Reservoir, 146, **147**
Rhizidiaceae, **375–377**
Rhizine, **516**
 nature of, 515
Rhizochloridales, **174–176**
Rhizochrysidales, **191–192**
Rhizodiniales, **163–164**
Rhizoid, **57**, 61, 95, **96**, 110, 122, **123**, **126**, 128, 180, **181**, **242**, 243, **272**, 273, 303, 328, 384, 395, 405, **406**
 initial of, **134**
 primary, **134**
 secondary, **134**
Rhizome, 108, **109**
Rhizomorph, 446, 475, **477**, 483
Rhizomycelium, 375, 381
Rhizophidium, **376–377**
 globatum, **376**, **377**
Rhizoplast, 17, 146, **147**, **152**, **157**, 158, 184, 188
Rhizopodial stage, 50
Rhizopodial tendency, 25
Rhizopus, **405–408**
 nigricans, **406**, **407**, 408
Rhodomela, 256
Rhodophyceae, 6, 277, 284, 285, **295–350**, 368
Rhodophyta, 10, **295–350**
 cell structure in, 296–297
 characteristics of, 8, 295
 classification of, 300
 distribution of, 295–296
 pigments of, 297- 298
 relationships of, **9**, 299–300, 422, 460
 reproduction of, 298 -299
 thallus structure of, 298
Rhodymeniales, **339- 342**
Rhoicosphenia curvata, **203**
Rhytisma, **440–442**
 acerinum, 440, **441**, **442**
Rivularia dura, **280**
Rod organ, **145**, 146
Rusts, 467, 469, 473, **493–502**
 autoecious, 494
 black, 496
 heteroecious, 494
 macrocyclic, **494–499**
 microcyclic, **500–502**
 orange, 500
 red, 494
 white, 402

S

Saccharomyces cerevisiae, **429**
Saccharomycetaceae, **427–430**
relationships of, **369**
Saccharomycodes Ludwigii, **430**
Saprolegnia, **391–394**, 398
ferax, **392**, 394
torulosa, 392
Saprolegniaceae, **391 394**
Saprolegniales, 374, **390–399**
relationships of, **369**
Sapromyces, **395–396**
androgynus, **395**
Reinschii, **395**
Sargassum, 220, 221, 224, 266, 267
natans, 224
Scale, siliceous, 187, 188
Scaphospora speciosa, 238, 239
Scenedesmaceae, 90, **101–102**
Scenedesmus, **101 102**
quadricauda, **101**
Schizogoniaceae, **60–62**
Schizogoniales, **60–62**
relationships of, **26**
Schizomeridaceae, **59–60**
Schizomeris, **59–60**
Leibleinii, **60**
Schizophycean phycoerythrin, 285
Schizosaccharomyces, **427–429**, 430
octosporus, 427, **428**, 429
Scinaia, 299, **321–325**
furcellata, **322, 323, 324**
Sclerotium, 354, 452, 483
development of, 453
germination of, **454**
Scytomonas, 148
Scytonema, 522
Semicell, **85**
Separation disk, **287**, 288
Septobasidium, **491–492**
pseudopedicellatum, **492**
retiforme, **492**
Sexual reproduction (*see* Anisogamy; Isogamy; Oögamy)
Shield cell, **131**, 132
Sieve plate, 263, 264
Sieve tube, 263, 264
Silicification, 179, 184, 187, 189, 200
demonstration of, 199
nature of, 199
Simultaneous cleavage, 20, 89
Sinus, **85**
Siphonales, 13, 26, 27, 62, **102–122**, 174
relationships of, **26**
Siphoneae verticillatae, 102, 125
Siphonocladiales, 26, 27, 62, **122–127**
relationships of, **26**
Slime molds (*see* Myxothallophyta)
Smut balls, 506
Smuts, 469, 473, **502–507**
Soralia, 518
Soranthera, **256–257**
ulvoidea, 256, **257**
Soredial dust, 518
Soredium, 517, **518**
Sorophore, **363**
development of, 364
Sorus, 145, **241, 242, 244, 257, 262, 363,** 364, 381, **403**, 494
female, **246**
male, **246**
Spermatangial filament, 331, **332**
Spermatangial mother cell, 308, 309, 316, **317**, 335, 344
Spermatangium, 299, 308, **317, 319, 321, 323, 326,** 331, 344
development of, 308
Spermatiophore, 438
Spermatium, 299, **303**, 305, 309, 316, **317,** 344, 416, 422, 434, 460, **461**, 494, 497, **498, 520**
development of, 304
liberation of, **303**, 304
Spermocarp, **52**, 53
nature of, 53
Spermogonium, 438, **439**, 497, **498**, 501, 519
nature of, 417
Sphacelaria, 220, 224, **235–237**
bipinnatus, 237
californica, **236**
radicans, **236**
Sphacelariales, 221, 225, **235–237**
relationships of, **229**
Sphacelia, 453
segetum, 453, 511
Sphacelial stage, **453**
Sphaeriales, 431, **455–458**
relationships of, **369**
Sphaeroplea, 14, 21, **65–68**
annulina, **66, 67**
cambrica, **66, 67**
tenuis, 68

Sphaeropleaceae, 62, **65–68**, 122
Sphaeropsidales, **512**
characteristics of, 512
Sphaerozosma Aubertianum var. *Archerii*, **87**
Sphenopsida, 5
Spindle organ, 381, **382**
Spirogyra, 14, 19, 21, 80, 81, 389
Spirogyrales, 373
Spirotaenia condensata, **83**
Sporangiophore, 400, **401**, 405, **406**, 409
development of, 405, **410**
Sporangiospore, 371
Sporangium, **54**, 55, 115, **117**, 118, **354**, **355**, **359**, 371, 381, **382**, 386, **395**, [illegible], 398
detachable, 55
development of, 115, 360, 384, **387**, 391, **392**, 405, **406**
initial of, 243
nature of, 19, 367
neutral, 227, **232**, 233, **234**, 239, 248, **249**, 250
development of, 225, **232**
nature of, 225
plurilocular, 224, 227, 233
nature of, 225
unilocular, 224, 225, 227, **232**, 233, 234, 235, **236**, 237, 238, **242**, 243, 244, **246**, **248**, 249, 250, **251**, **254**, 255, 256, **257**, **258**, 259, **262**, 264
development of, 224, 231, 264
nature of, 224
Spore, **358**, **362**
germination of, **356**, **359**, 360, **362**, **363**, 364
(*See also* Aecidiospore; Aplanospore; Ascospore; Basidiospore; Conidium; Monospore; Paraspore; Polyspore; Teleutospore; Tetraspore; Uredospore; Zoospore)
Spore-producting plants, 1–10
classification of, 5–9
interrelationships among, **9**, 10
nature of, 2
Sporochnales, **250–252**
relationships of, **229**
Sporochnus, 250
Sporodochium, 416
Sporophore, 357, **358**, **359**
Sporophyll, 259
Sporophyte, 222, 223, 226, **227**, 233, **234**, 235, **238**, 243, **248**, **249**, **251**, **253**, **257**, **258**, 261, **262**, 264, 268
of Basidiomycetae, 466
development of, **242**, **252**, **254**, 255, **265**, 266, **272**, 273
Stalk cell, **133**, **347**, **495**, **496**
primary, **241**, 243, **246**
Starch, **16**, 61, 95, 116, 151, 153, 156, 164, 297, 366, 368
formation of, 15
stroma, 69
Statolith, 87
Statospore, 7, **172**, 183, **184**, 189, **193**, 195, **208**
binucleate, 191
formation of, **172**, **185**
germination of, 173
structure of, **184**
Staurastrum curvatum, **85**
fœcigerum, **88**
Stemonitis splendens, **354**
Stephanokontae, 68
Sterigma, 400, **401**, **432**, **469**, 471, **479**
Sterile filament, **346**
initial of, **345**
Sticta, **516**
Stigeoclonium, **49–50**
lubricum, **49**
tenue, **49**
Stigmatomyces, **460–462**
Baeri, 460, **461**, 462
Stipe, **262**, **475**, **477**, **483**
Stipule, 129, **133**
Stolon, 405, **406**
Stroma, **454**, **459**
Subhymenium, 522
Suffultory cell, 74, **76**
Sugar, 222
Sulcal plates, **162**
Sulcus, **159**, 163
Summer spore, 378, 379, **380**
Supporting cell, 308, **335**, **340**, 341, 344, **345**, **346**
Suspensor, **407**, 408
Suture, 156, **162**
Symbiosis, 513
Synchytriaceae, 375, **379–381**
Synchytrium, 375, **380–381**
endobioticum, **380**

Synura, **188–189**
Adamsii, **189**
uvella, **189**

T

Tabellaria fenestrata, **200**
Taphrina, **450–452**
carnea, 450
Coryli, 451
deformans, 450, **451**
epiphylla, **451**
Johansonii, **451**
Pruni, 450
Teleutosorus, **496**
Teleutospore, 493, **496**, 499, 502
development of, **496**
germination of, 497, **498**, **500**
Tetradinium minus, **166**
Tetraedron, **100–101**
minimum, **100**
Tetraspora, **40–42**
cylindrica, **41**
gelatinosa, **41**
Tetrasporales, 15, 26, 27, **40–42**, 164. 174
relationships of, **26**
Tetrasporangium, 311, 321, **326**, 328, 331, **333**, **334**, 335, **338**, 342, **347**
Tetraspore, of Phaeophyta, 244
of Rhodophyta, 299, 306, 311, **326**, 331, **333**, **334**, 335, **338**, 342, **347**
germination of, **326**, 328, 342
Tetrasporine tendency, 25
Tetrasporophyte, 311, **313**, 314, 328, 331, **333**, 335, 338, 342, **347**
Thallophyta, 2
characteristics of, 2
validity of, 2
Theory of vegetative tendencies, 25
Tilletia, **505–507**
foetans, 505
Tritici, 505, **506**
Tilletiaceae, **505–507**
Tilopteridales, **237–239**
relationships of, **229**
Tolypothrix tenuis, **280**
Trabecula, 106, **107**
Trachelomonas volvocina, **145**
Tracheophyta, 5
Trama, **478**
Trebouxia, **91–92**
Cladoniae, 91, **92**
Tremella, **489–490**
frondosa, **489**
lutescens, 489
mesenterica, 489
mycetophila, 489
Tremellales, 473, **487–490**
relationships of, **369**
Trentepohlia, 15, 19, **54–56**
aurea var. *polycarpa*, **54**
Trentepohliaceae, **54–56**
Tribonema, 47, 169, 173, **177–179**
bombycinum, 170, **178**
Trichoblast, **152**, **343**, 344
carposporangial, 344, **345**
tetrasporangial, 343, 344
spermatangial, **343**, 344
Trichogyne, **52**, 53, 299, 308, 309, **317**, **319**, **321**, **324**, **327**, **329**, **330**, **332**, **335**, 336, **337**, **340**, 344, **345**, 417, **418**, 422, 438, 441, **443**, 444, **457**, 461, 519, **520**
Trichome, 279, **280**, 281, 288, 291
Trichothallic growth, 223, **240**, **242**, 247, **248**, **249**, 250, **252**, **254**
nature of, 223
Tube cell, **133**
Tuber, **445–448**
candidum, **446**, **447**, **448**
melanosporum, 445, 446
Tuberales, **445–448**
relationships of, **369**
Turbinate organ, 381, **382**

U

Ulothrix, 19, 20, 23, **44–45**
zonata, **44**, 45
Ulotrichaceae, **43–45**
Ulotrichales, 15, 23, 27, **42–56**, 62, 69, 81, 174
relationships of, **26**
Ulva, **56–59**, 248
lobata, **57**, 59
stenophylla, **57**
Ulvaceae, 24, 25, 27, **56–59**
Ulvales, 27, **56–60**
relationships of, **26**
Urceolus cyclostomus, **145**
Uredinales, **493–502**
relationships of, **369**
Uredo, **402**
Uredosorus, 494, **495**

Uredospore, 494, 511
 formation of, **495**
 germination of, **495**
Urospora, 25, 63
Ustilaginaceae, **502–505**
Ustilaginales, **502–507**
 relationships of, **369**
Ustilago, **502–505**
 anthearum, **466**
 Carbo, **466**
 Vuijckii, 503
 Zea, **503, 504, 505**

V

Vacuoles, 86, 155
 central, 14, 103, 108, 123, 130, 296
 contractile, 14, **29**, 30, 35, 48, **152**, 172, **174**, 183, 188, 190, 193
Valonia, **122–124**
 Aegagropila, **123**
 macrophysa, **123**, 124
 utricularis, **123**
 ventricosa, 122
Valoniaceae, **122–124**
Valve, of diatoms, 198, 199, **200**
 of Dinoflagellates, **154, 162**
Vaucheria, 16, 19, **116–120**, 373
 sessilis, **120**
Vaucheriaceae, 102, **116–120**
Vaucheriales, 373
Vegetative multiplication, 48, 49, 60, 61, 66, 72, 95, **96**, 107, 130, 224, 287, 298
Velum, **477**, 478
Ventral plate, 161
Venturia, **455–458**
 inaequalis, 455, **456, 457, 511**
Vicia unijuga, 378
Volutin, 196, 204
Volva, inner, **483**, 484
 outer, **483**, 484
Volvocaceae, 27, **31–40**
Volvocales, 15, 18, 20, 23, 26, 27, **28–40**, 164
 colonial, **31–40**
 relationships of, **26**
 unicellular, **29–31**
 relationships of, **26**
Volvocine tendency, 25
Volvox, **17**, 18, 26, 32, **36–40**
 aureus, **36**, 40
 capensis, 40

W

Walls, unsegmented, 83
Water bloom, 277
Westiella lanosa, **287**
Winter spore, 378, **379**, 380
 germination of, 379, 381
Woroninaceae, 375, **382–384**

X

Xanthidium antilopaeum var. *polymazum*, **85**
Xanthophyceae, 3, 6, 7, 95, 116, 158, 164, 165, **168–182**, 186, 204, 208
 asexual reproduction of, 171–173
 cell structure in, 169–171
 characteristics of, 168
 classification of, 173
 distribution of, 169
 evolution of, 173
 sexual reproduction of, 173
Xanthophyll, 221

Yeasts, 424, **427–430**
 budding, 427, **429**
 fission, 427

Z

Zanardinia, 239
Zonaria, 222, 223, **244–247**
 Farlowii, **244**, 245, **246**
Zoogamete, 30, **31**, **33**, **41**, 42, **44**, 50, 55, **57**, 58, **64**, 65, 91, 92, 94, 95, **96**, **104**, **110**, 112, **113**, 148, **173**, 178, 182, 191, 214, **232**, 257, 259, 352, **356**, 357, **359**, 360, 361, 367, 368, 369, 372, 375, 381
 female, **377, 385**
 formation of, **57**, 58
 liberation of, 58, **64**, 112, 113
 male, **377, 385**
 nature of, 21, 367
Zooids, 27, 35, 96, **107**, 123, **148**, 149
 nature of, 16
 liberation of, **378**
 stephanokontean, 68, **73**, 74

Zoospore, 19, 23, 26, 42, **44**, 45, **46**, 48, **49**, 52, **54**, 55, 58, 59, 60, 64, 68, 72, **73**, **91**, **95**, **99**, **153**, 159, **161**, **163**, 164, **165**, **166**, **171**, 172, 176, **178**, **180**, 181, **185**, 186, 188, 189, 190, **193**, 194, **195**, 214, 224, 227, 228, 233, 234, 237, 250, 261, 267, 271, 368, 371, 375, **376**, **382**, **383**, **385**, **387**, **389**, 390, 391, 395, 398, **401**, **403**, **404**
formation of, 20, 46, 49, 58, 72, **91**, 92, **389**, **397**
germination of, 68, **73**, **113**, 114, **117**, 120, **178**, **193**, 255, 265, **382**, **401**, **403**
liberation of, 20, 53, 60, 64, **73**, **95**, 98 99, **117**, 165, 166, 231, 264, 375, **376**, **382**
multiflagellate, 116, **117**
nature of, 118
neutral, 225
stephanokontean, **115**
swarming of, 20, 98, **99**, 177

Zygnema, 19, **22**, **79–83**
Zygnemataceae, 13, 27, **79–83**
Zygnematales, 21, 23, 27, **78–89**, 373
relationships of, **26**
Zygomycetae, 374
Zygomycetes, 373, 374
Zygosaccharomyces, 430
Barkeri, 429, **430**
Zygote, **31**, **39**, **41**, **44**, 50, **52**, 53, 59, **67**, 68, **75**, 77, **80**, **84**, **88**, **96**, 97, **99**, **120**, 133, 161, 181, 182, 191, 209, **210**, **211**, 212, 214, 226, 233, 242, **272**, 299, **356**, **359**, 360, 364, 367, **377**, **379**, **383**, 384, **387**, **389**, **393**, **395**, 396, **399**, **404**, **407**, **411**, 417, **428**, 511
germination of, 22–23, **31**, 34, 36, **39**, 42, 45, **52**, 53, 59, 65, 68, **77**, 78, **82**, 83, **84**, **88**, 89, 94, **99**, 105, 110, 125, 133, **134**, **252**, 255, 266, **272**, 273, 372, **379**, **380**, **387**, 388, 390, 394, 399, **401**, 402, **404**, **407**, 408